MADROÑO

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DEDICATION

Harold A. Mooney is synonymous with plant ecology in California. Trained initially as a physiological ecologist, Hal has made significant contributions over the past four decades to all aspects of ecology and to the advancement of plant sciences throughout California. Immediately following his Ph.D. dissertation, under Dwight Billings at Duke University, he moved to UCLA where he continued his pioneering research on the ecophysiological differentiation among ecotypes of alpine species. Soon thereafter Hal and his students moved to Stanford, where they expanded their efforts to include ecological studies of chaparral species; this was quickly followed by the development of an integrated program to study convergent evolution among Mediterranean-climate plants of California and Chile. In the 1970's Hal's research focus expanded further to include ecophysiological and biochemical studies of how plants adapt to extreme environments. His pioneering field studies of how plants adapt to the harsh desert climate of Death Valley were among the first to bring sophisticated laboratory-based measuring systems to the field. Today he and colleagues are focusing on California grassland ecosystems, examining how plants and their communities will respond to elevated carbon dioxide concentrations. Hal is one of the leading advocates for studies of global climate change and a strong proponent for integrated, experimental field studies. Throughout his career, he has been a pioneer and an inspiration to us all. It is with great pleasure that we dedicate this volume of Madroño to Harold A. Mooney in appreciation of his contributions to the advancement of California plant sciences.

TABLE OF CONTENTS

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MADROÑO

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Contents

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UTILITY OF GROWTH RINGS IN THE AGE DETERMINATION OF CHAPARRAL SHRUBS

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Abstract

Use of plant growth rings for age determination requires distinct rings and verification that these are produced annually. In this study of southern California chaparral shrubs, the sharpest rings were produced by shallow-rooted, non-sprouting species of *Arctostaphylos* and *Ceanothus*. The least distinct rings were produced by the deep-rooted resprouting shrub *Malosma laurina*. Ring counts on stems from stands of known age indicated that on some sites the majority of shrubs can be accurate indicators of stand age; but, some may not be. Non-sprouting species of *Ceanothus* and *Arctostaphylos* were good indicators of stand age as stems generally did not deviate from stand age by more than 5%. However, in older stands a large proportion of these taxa could not be aged due to heartrot. Some stems on resprouting shrubs deviated widely from stand age. Interpretation of this pattern is complicated by the often continuous nature of stem recruitment in years subsequent to fire and thus, many of the stems (ramets) of such species will not be an accurate measure of the shrub (genet) age. At one site, an indirect technique was used to show that shrubs are not producing extra "false rings" or are not missing rings. At this site there was a marked synchrony of maximum ring width for the same year for six species. This ring was the widest, out of the last 16 rings, and coincided with one of the highest rainfall years in recent history.

Growth rings have proven to be an invaluable resource for age determination in woody plants. The technique requires the presence of growth rings with a clear demarcation between spring wood and summer wood and the verification that these are produced annually. Studies in the southwestern U.S. have verified the annual nature of growth rings in trees and shrubs of some species (Stokes and Smiley 1968; Ferguson 1959, 1964; Roughton 1972; Arno and Wilson 1986). However, the technique does not work well on all species or all individuals of a species; some do not produce discernable growth rings and others, with distinct growth rings, do not reliably produce a single ring annually (e.g., Ferguson 1959; Roughton 1972; Carlquist 1980).

Most chaparral shrubs produce a growth ring in which spring and summer wood are distinguishable (Webber 1936; Watkins 1939; Fishbeck and Kummerow 1977; Carlquist 1980; Kummerow et al. 1981; Michener 1981). Species differ, however, in being ring porous or diffuse porous, in the cells which produce the ring pattern and the distinctness in the ring boundary. Several studies of chaparral have used growth rings to determine age (Sampson 1944; Hedrick

1951; Patric and Hanes 1964; Stocking 1962; Keeley 1975; Guntle 1974; Schlesinger and Gill 1978; Kummerow et al. 1981; Hubbard 1986; Montygierd-Loyba and Keeley 1986) although verification of their annual nature has usually been lacking. Due to the seasonal growth conditions imposed by the mediterranean climate, the assumption of annual ring deposition seems justifiable. Verification, however, is the *sine qua non* for accurate age determination by ring counts because two growth anomalies are possible (Fritts and Swetnam 1989). In years of extremely low rainfall, cambial growth may be limited to the extent that a growth ring will not be laid down. Failure to recognize such "missing rings" will underestimate the age of a stem. In some years, renewed growing conditions near the end of the growing season can result in an additional spurt of growth and laying down of an additional "false ring." Failure to recognize false rings will overestimate the age of a stem.

The purpose of this study was to determine which chaparral species produce discernable growth rings and evaluate to what extent they could reliably be called annual rings. Two approaches were taken. One was to determine the age of the largest stem on chaparral shrubs from sites of "known" age. The other part of this study was to evaluate an indirect measure of the extent of false or missing rings. Ring width, which often reflects climatic favorableness, was measured on the dominant shrubs for each of the last 16 rings. If rings are faithfully laid down each year there should be a degree of synchrony in growth ring width among species that is correlated with climatic conditions, in particular, precipitation.

Study Sites and Methods

For the first part of this study, stands of known age were selected from fire maps produced by the Los Angeles County Fire Department, Forestry Division, the USDA Forest Service, Angeles National Forest and historical records in Minnich (1987). Due to the large scale at which such maps are made, and the potential for wildfires to leave unburned islands of vegetation within their boundaries, this technique of ascribing stand age carries with it some potential for error.

Five sites, of 9, 24, 28, 65 and 88 years of age at the time of sampling (fall 1984), were selected. The locations were as follows: 1) The Clear Creek Fire burned in 1975 in the San Gabriel Mtns (Los Angeles Co.) near the Clear Creek Forestry Station. Plants were sampled N of Angeles Crest Hwy at the Clear Creek Overlook (1100 m). 2) The Johnstone Fire burned much of the San Dimas Experimental Forest (Los Angeles Co.) in the San Gabriel Mtns in 1960. Plants were sampled above Bell Canyon (800 m). 3) The Sherwin Fire burned an extensive portion of the western end of the Santa

Monica Mtns (Ventura Co.) in 1956. Shrubs were sampled along Yerba Buena Rd (600 m). 4) The San Gabriel Fire burned much of the San Gabriel Mtns (Los Angeles Co.) along the Glendora Mtn Rd. and Glendora Ridge Rd. in 1919. Plants were sampled near the junction of those two roads (975 m). 5) In 1896 a massive fire burned most of the chaparral along the Angeles Forest Highway (Los Angeles Co.). Although much of the area burned again in the early 1980's, a pocket of vegetation was untouched and this site, ½ km N of the Monte Cristo Ranger Station (1000 m), was sampled.

In the field a stem section of several cm thickness was cut at ground level. Depending upon the community composition, two to six species were sampled from each site. For each species five or more shrubs were sampled. Many plants had more than a single stem and on these the largest stem was sampled. In the lab, stem sections were polished with high grade (200–300 grit) sandpaper on a belt sander. To make growth rings more readily distinguishable, various techniques were utilized that accentuated the spring wood from the summer wood. These included applying one of the following: water, linseed oil, kerosine or paraffin oil. Distinguishing growth rings on some species, e.g., *Adenostoma fasciculatum,* was sometimes difficult due to dark coloration of the heartwood. Soaking overnight in 5.25% sodium hypochlorite solution bleached out this color. Growth rings were counted under a dissecting microscope at 7–10× power by two independent observers.

The site for the second part of this study was in Silverado Canyon in the Santa Ana Mtns (Orange Co.) at 950 m. According to USDA Forest Service, Cleveland National Forest records, no fire had ever been recorded from this site. Stem sections were collected in fall 1983 from all of the dominant species and treated as described above. Ring width was measured for the last 16 rings on each stem with a micrometer. If these rings were laid down annually, this time period would have included exceptionally wet and exceptionally dry years (data from NOAA 1968–1984).

Nomenclature is according to Munz (1959) except for *Malosma laurina* (Nutt.) Nutt. ex Abrams. (*Rhus laurina* Nutt.).

RESULTS

The following shrubs produced recognizable growth rings: *Adenostoma fasciculatum, Arctostaphylos glauca, Ceanothus* spp., *Cercocarpus betuloides, Garrya veatchii, Heteromeles arbutifolia, Prunus ilicifolia, Quercus dumosa,* and *Rhamnus crocea* ssp. *ilicifolia.* Some species with diffuse porous wood had less distinct boundaries between rings, making counts difficult and the most difficult were *Rhus ovata* and *Malosma laurina. Quercus dumosa* was confusing at first because bands of parenchyma cells were often laid down in waves

Fig. 1. Cross section of *Ceanothus megacarpus* stem illustrating distinct annual growth rings.

during the growing season. Summer wood was, however, character-ized by the production of a dense layer of narrow vessels.

One characteristic that separated all of these taxa was the sharpness of the boundary between the spring and summer wood. The most distinct growth rings were produced by obligate-seeding taxa of *Ce-anothus* (Fig. 1) and *Arctostaphylos*.

One approach to verifying that growth rings were produced an-nually was to examine ring counts on stems from stands with known fire history (Table 1). At each site there were some shrubs with ages reflecting the time since the last fire. Shrubs deviating from this pattern need to be evaluated carefully. Deviation from stand age may be due to missing or extra rings, or due to recruitment of stems in years subsequent to fire. The latter factor may be very significant for postfire resprouting taxa, e.g., *Adenostoma, Cercocarpus, Garrya, Heteromeles, Quercus, Prunus,* and *Rhamnus.* Although the term resprouting derives from the fact that they regenerate vegetatively from the rootcrown after fire, these shrubs are capable of continuous recruitment of stems during the fire-free period. This is illustrated by the age structure of all stems on a single *Adenostoma fasciculatum* shrub (Fig. 2); plant #1 had several stems that date back to near the time of the last fire and apparently stems have established every few years since that time.

Non-sprouting species of *Ceanothus* and *Arctostaphylos* do not
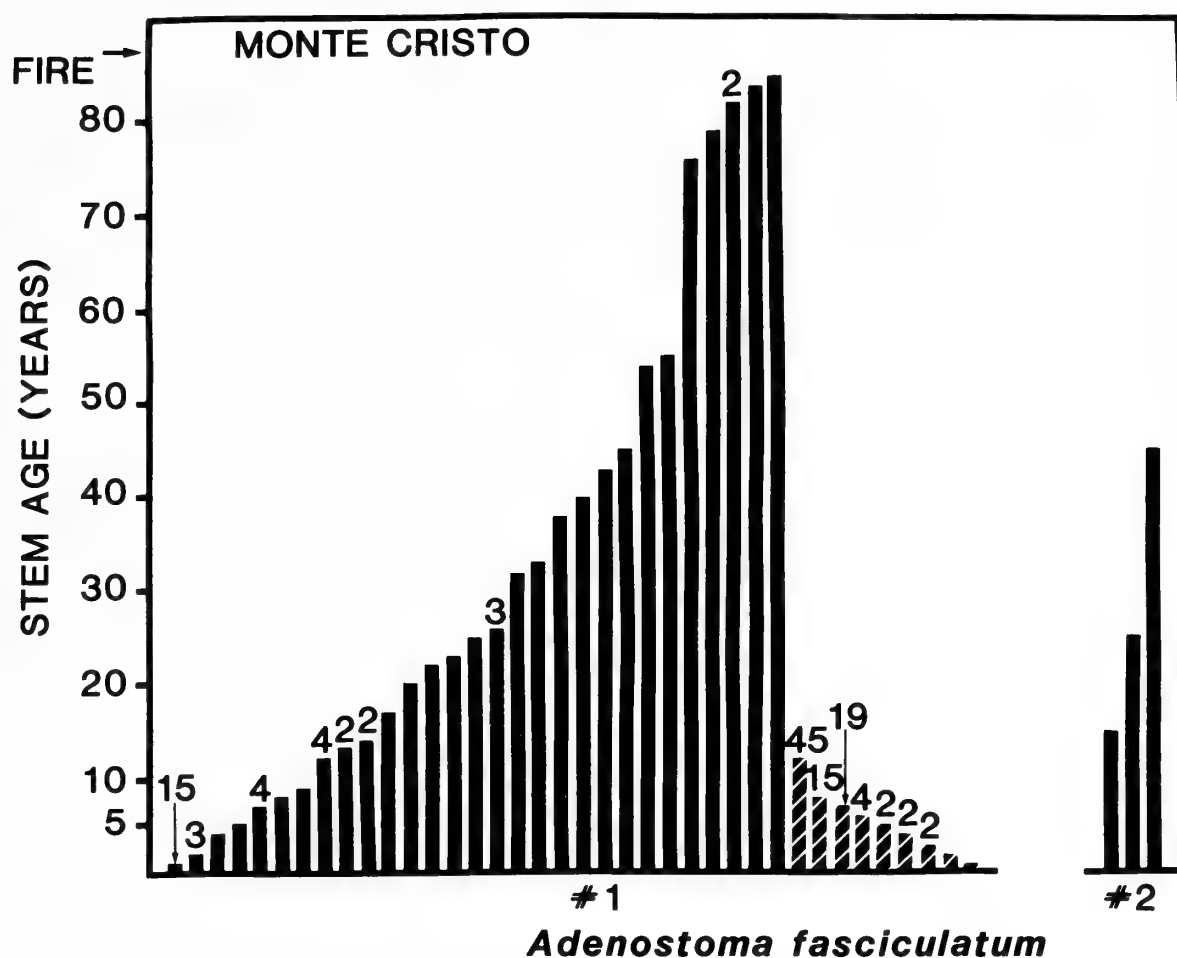
FIG. 2.   Age distribution of all stems on two *Adenostoma fasciculatum* shrubs from the Monte Cristo Site. Each solid bar represents one live stem; a number above the bar signifies more than one stem. Cross-hatched bars represent dead stems.

regenerate vegetatively and thus, in the absence of seedling recruitment between fires, all stems should be seen to date back to the time of the last fire, assuming of course that the heartwood is not rotted. There was only one exception (at the Sherwin Site) to the generalization that deviations from stand age were ≤5% for these non-sprouting taxa.

Another approach used to verify the annual deposition of growth rings was to look for synchrony in growth response between plants at the same site. In exceptionally wet years, very wide growth rings are laid down and in exceptionally dry years very narrow rings are produced. If such a 'finger-print' is synchronous among a significant number of plants at a site it is taken as evidence that growth rings are responding to the same annual variations in climate and reflecting annual growth rings. At the Silverado Site the ring width was measured for the last 16 growth rings on stems of six species. Although annual ring width over the entire 16 years was not highly synchronized between plants (data not shown), one extremely good year and several bad years were synchronized between different species at the site (Table 2). For 23 of the 24 stems examined, the 15th

TABLE 1. NUMBER OF GROWTH RINGS ON THE LARGEST STEM FROM SEPARATE SHRUBS COLLECTED IN THE FALL OF 1984 FROM SITES WITH KNOWN FIRE HISTORY. Postfire mode of regeneration; OR = obligate resprouter, FS = facultative seeder, OS = obligate seeder.

| | | | | Shrubs deviating from stand age | | |
| | | % of shrubs dated to last fire | | | | % deviation from stand age |
Species	Post-fire mode*	%	(n)	Number of shrubs	Number of growth rings	
Clear Creek Fire (Burned 1975)						
Quercus dumosa	OR	100	(5)	0		
Cercocarpus betuloides	OR	40	(5)	3	8	−11
Johnstone Fire (Burned 1960)						
Ceanothus crassifolius	OS	80	(5)	1	23	−4
Quercus dumosa	OR	60	(5)	2	23	−4
Sherwin Fire (Burned 1956)						
Ceanothus crassifolius	OS	60	(10)	2	29	+4
				1	27	−4
				1	15	−46
Adenostoma fasciculatum	FS	0	(22)	9	27	−4
				6	26	−7
				4	25	−11
				3	24	−14
San Gabriel Fire (Burned 1919)						
Ceanothus crassifolius	OS	80	(5)	1	44 (heartrot)	—
Arctostaphylos glauca	OS	40	(5)	1	64	−2
				1	60 (heartrot)	—
				1	56 (heartrot)	—
Heteromeles arbutifolia	OR	100	(2)	0		
Adenostoma fasciculatum	FS	33	(6)	1	62 (heartrot)	—
				2	49	−25
				1	36	−45
Garrya veatchii	OR?	0	(1)	1	29	−55
Prunus ilicifolia	OR	0	(1)	1	54	−17
Monte Cristo (Burned 1896)						
Arctostaphylos glauca	OS	33	(6)	1	86	−2
				1	84	−5
				1	69 (heartrot)	—
				1	62 (heartrot)	—
Ceanothus crassifolius	OS	0	(6)	1	78 (heartrot)	—
				1	77 (heartrot)	—
				1	71 (heartrot)	—
				1	64 (heartrot)	—
				1	59 (heartrot)	—
				1	51 (heartrot)	—

TABLE 1. CONTINUED.

| Species | Post-fire mode* | % of shrubs dated to last fire | | Shrubs deviating from stand age | | |
		%	(n)	Number of shrubs	Number of growth rings	% deviation from stand age
Adenostoma	FS	0	(5)	1	85 (heartrot)	—
fasciculatum				1	84	−5
				1	75	−15
				1	54 (heartrot)	—
				1	45	−49

ring (from the perimeter) was the widest, and in all but one case it was followed by a year with a significantly narrow ring. Ring 15 would have been laid down in the very wet winter and spring of 1969 (precipitation for January, February and March was 224% above normal for the nearest station at Santa Ana). The following year had a very narrow band, as did 1972 and 1981, and these years had 52%, 48% and 60%, respectively, of the average rainfall.

DISCUSSION

Rings with a clear demarcation between spring and summer wood are evident in the obligate-seeding species of *Arctostaphylos* and *Ceanothus* (Fig. 1). These non-sprouting taxa have relatively shallow root systems, dating back to establishment as seedlings after the last fire, and consequently are exposed to much lower soil water potentials during the summer drought than are sprouting species (Miller and Poole 1979; Barnes 1979; Schlesinger and Gill 1980; Parsons et al. 1981). In non-sprouting species, stomatal closure may persist for months (Poole et al. 1981), resulting in a sharp cessation in cambial growth and deposition of very narrow vessels (Carlquist 1980). The only report of obscure boundaries between growth rings in obligate-seeding taxa is for two *Arctostaphylos* species from southeastern Arizona (Harlan 1977). The presence of substantial summer rains in that region may account for the difference in distinctness of growth rings from that observed for southern California taxa.

Shrubs with deeper roots sometimes have less distinct rings and this may be tied to the continuation of cambial growth through the summer as observed for *Rhus ovata* (Avila et al. 1975). In the present study growth rings were visible, although not always distinct in *Rhus*. *Malosma laurina* produced the least discernable growth ring, due to its diffuse porous wood (Young 1974). Watkins (1939) noted that annual rings were poorly defined in young twigs of *Adenostoma fasciculatum* and *Prunus ilicifolia*. Observations made in the present study do not concur, and other investigators have reported distinct

TABLE 2. RELATIVE RING WIDTHS FOR SELECTED YEARS FROM 1968 TO 1983 FOR SPECIES CUT IN FALL 1983 FROM THE SILVERADO SITE. For each stem, ring widths were measured and normalized to the widest ring width observed across the last 16 years of rings. Years 1968–1970 are underlined to emphasize the synchrony in growth observed between species.

Species	Stem age	Relative ring width								
		1968	1969	1970	1971	1972	...	1981	1982	1983
Adenostoma fasciculatum										
#1	(41 yr)	42	100	25	33	16	...	16	33	16
#2	(41 yr)	54	100	23	31	69	...	15	38	23
#3	(32 yr)	60	70	30	30	15	...	20	70	70
#4	(41 yr)	75	100	38	38	50	...	13	38	25
#5	(54 yr)	81	100	100	36	36	...	27	46	46
#6	(47 yr)	57	100	29	57	14	...	29	31	38
Quercus dumosa										
#1	(100 yr)	62	100	46	85	85	...	23	31	38
Ceanothus crassifolius										
#1	(117 yr)	60	100	20	50	10	...	30	50	10
Rhamnus crocea										
#1	(117 yr)	18	100	20	50	10	...	30	50	10
#2	(88 yr)	20	100	33	33	22	...	11	56	78
#3	(53 yr)	44	100	33	13	13	...	20	13	13
#4	(59 yr)	20	100	21	21	21	...	21	14	43

TABLE 2. CONTINUED.

Species	Stem age	1968	1969	1970	1971	1972	...	1981	1982	1983
Heteromeles arbutifolia										
#1	(100 yr)	42	100	17	8	25	...	33	17	42
#2	(51 yr)	25	100	13	6	50	...	13	50	75
#3	(106 yr)	60	100	40	6	6	...	6	20	20
#4	(55 yr)	50	100	25	50	75	...	38	25	25
#5	(86 yr)	60	100	70	60	80	...	30	20	20
#6	(83 yr)	83	100	33	17	50	...	17	17	17
Rhus ovata										
#1	(57 yr)	40	100	10	20	40	...	30	40	30
#2	(43 yr)	36	100	54	73	18	...	27	27	27
#3	(73 yr)	71	100	71	71	71	...	57	57	86
#4	(43 yr)	57	100	57	29	14	...	43	71	86
#5	(69 yr)	36	100	9	18	9	...	27	36	46
#6	(61 yr)	21	100	29	29	21	...	21	29	21

Relative ring width

growth rings in *A. fasciculatum* (Sampson 1944; Stocking 1962; Kummerow et al. 1981).

Studies of the southern Californian chaparral tree *Pseudotsuga macrocarpa* have revealed that absent rings comprised less than 1% of the total rings and false rings were virtually absent (Schulman 1947; Michaelsen et al. 1987). The lack of false rings was attributed to the absence of summer precipitation and, based on ring counts of chaparral stems from stands with known fire history (Table 1), false rings are apparently uncommon in chaparral shrubs; two *Ceanothus crassifolius* at the Sherwin Site did have an "extra" ring each (Table 1). Missing rings, however, might be expected to be more common because the shallow root systems of chaparral shrubs would make cambial growth very sensitive to dry years (Kummerow et al. 1981). Data from Table 1 suggest that for non-sprouting *Ceanothus* and *Arctostaphylos,* missing rings may result in a few percent error when assigning ages based on ring counts.

Interpreting data from Table 1 for sprouting taxa such as *Adenostoma* is more complicated. Some stems give ring counts close to the age of the stand (based on known fire history) but some have many fewer rings. This could be due to a high frequency of missing rings or these stems may have been produced in years subsequent to the fire. The latter is certainly true for many of the stems on resprouting shrubs (e.g., plant #1, Fig. 2). The pattern illustrated by plant #2 (Fig. 2) requires careful analysis. No stem on the plant dates back to within 44 years of the last fire. Three hypotheses could account for this pattern: 1) This plant established from seed 44 years after the last fire, 2) stems initiated after the last fire have died and fallen from the plant, or 3) this shrub has been highly suppressed and is missing many growth rings. The first hypothesis is unlikely since this species has not been observed to successfully recruit seedlings under the canopy of mature chaparral (Keeley 1992); however, an occasional seedling recruited in canopy gaps cannot be ruled out. Based on the generally slow rates of wood decomposition in chaparral (Gray and Schlesinger 1981), the second hypothesis also seems unlikely. Consistent with the third hypothesis is the fact that plant #2 was smaller in stature and seemingly less vigorous than surrounding shrubs. Future research needs to determine the extent to which suppression by competitors may suppress growth and thus suppress annual ring deposition in chaparral shrubs.

One seemingly anomalous growth ring pattern observed in another study (Keeley 1992) was the presence in an *Adenostoma sparsifolium* stem of 40 more growth rings than observed in any other species at the site; two *Ceanothus greggii* and one *Adenostoma fasciculatum* had maximum ages of 65 yr, whereas one *A. sparsifolium* had a stem that dated back 105 yr. This plant, however, apparently survived the last fire at the site and in fact had a very distinct fire scar 40 yr
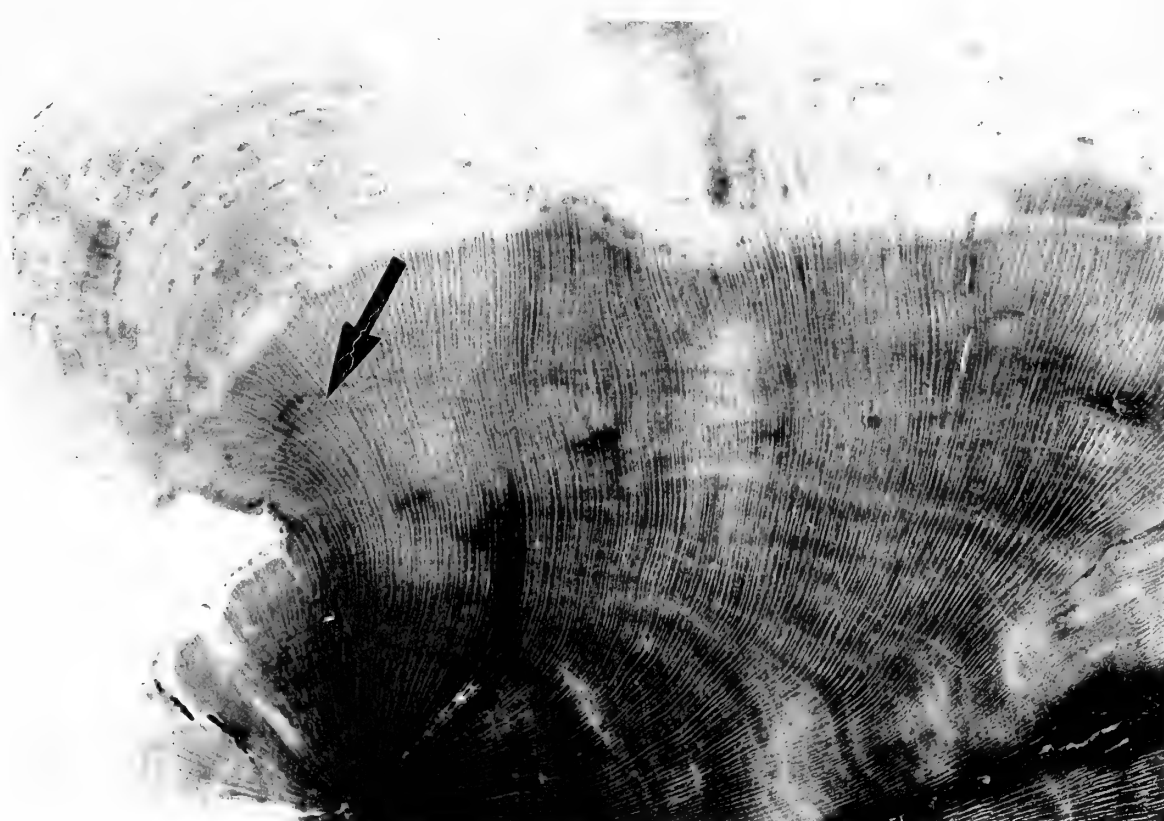
FIG. 3.   Cross section of *Adenostoma sparsifolium* stem aged at 105 yr. Arrow indicates a fire scar at 65 yr of age, which is the maximum age of all other stems counted at the site (Keeley 1992).

earlier (Fig. 3). Such fire scars are common in conifers but are not expected in chaparral shrubs since it is rare for a shrub to survive a wildfire. The arborescent nature of *A. sparsifolium* and the more open nature of the interior chaparral site where this plant came from may account for this unique phenomenon (Fig. 3).

A technique often of use in evaluating the extent of missing or false rings is called "cross-dating" (Stokes and Smiley 1968; Fritts and Swetnam 1989). It is based on two principles: 1) annual variations in climate (predominantly precipitation in the southwest) are reflected in variation in ring width, i.e., a year of high rainfall produces a wide growth ring whereas a year of low rainfall produces a narrow ring, and 2) there is a synchrony between different trees in a locality or region. After examining sequences of good and bad years for a substantial number of trees, a master chronology is developed to which all ring chronologies in a region are compared. For any particular site, deviations in alignment (with the master chronology) of good or bad years is accounted for by either taking out presumed 'false' rings or adding presumed 'missing' rings.

A priori one might predict chaparral shrubs would not be readily amenable to cross-dating. Based on extensive dendrochronology studies, it is commonly accepted that cross-dating is not likely to be successful on sites where plants are in close competition, as this

may override climatic signals (Glock 1937, Stokes and Smiley 1968). Competitive effects are likely a dominant factor controlling growth of chaparral shrubs (Schlesinger and Gill 1978, 1980). Substrate may also influence synchrony of growth response. In chaparral, marked heterogeneity in subsurface topography results in much diversity in rooting depths from one microsite to another (Kummerow 1981). This is likely to produce very different water relations between plants in the same community, even within the same species (Schlesinger and Gill 1980) and thus different growth responses. Another factor making cross-dating less feasible in shrubs is the shorter lifespan which provides fewer rings for matching. One attempt to cross-date shrubs from two sites in this study with a known regional chronology (developed by The Laboratory of Tree Ring Research, University of Arizona) produced equivocal results (Keeley unpublished data). However, the demonstration of marked synchrony to the extremely wet year of 1968 at the Silverado Site (Table 2) lends support to the conclusion that these shrubs do lay down annual rings and that the missing rings introduce a relatively small error.

In summary, there is good evidence that for many shrubs growth rings give a close approximation of age, although in general it would be premature to place high confidence in assigning precise years to most rings. Comparisons with stands of known age suggest that for the non-sprouting species of *Ceanothus* and *Arctostaphylos* there may be ≤5% error. The observation of ring counts for *Adenostoma fasciculatum* indicate the possibility that the error is greater, however, since resprouts can be initiated in years subsequent to the first postfire season, the deviation from stand age may be a function of recent recruitment and not due to missing rings.

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ADDITIONS TO THE FLORA OF THE SIERRA DE LA LAGUNA, BAJA CALIFORNIA SUR, MEXICO

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Abstract

The plant communities of the Sierra de La Laguna exhibit not only biological importance, but also socioeconomical importance to the peninsula of Baja California. This contribution is part of a project leading to establishment of an ecological preserve in such mountains. This work presents 48 additions to the flora of the woodland communities, 44 species are properly new additions, and 4 are reidentified taxa reported in a former paper. Most of the species (65%) are both annual and perennial herbs. An affinity geographical analysis of the total vascular plants of the woodland (272 species), shows that the community has high levels of affinity with the tropical flora at both family and genus level (39 and 37%, respectively), followed by the cosmopolitan flora (27 and 37%, respectively). The relatively high affinity with the cosmopolitan flora suggests a recent arrival of this flora in the woodland.

Resumen

Las comunidades vegetales de la Sierra de La Laguna presentan importancia no sólo biológica, sino también socioeconómica para la región sur de la península de Baja California. El presente trabajo forma parte de un proyecto más amplio que tiene como objetivo establecer una área para preservarse ecológicamente sobre tal serranía. Se presentan 48 adiciones a la flora del bosque de pino-encino y bosque de encino de la misma. Del total de adiciones, 4 son taxa reidentificados, y 44 son propiamente nuevos registros. La mayor parte de las especies (65%) corresponde a herbáceas. Un análisis de afinidad geográfica en el total de las especies vasculares de esta comunidad (272 especies) revela que se guardan relaciones estrechas con la flora de afinidad tropical tanto a nivel de familia como de género (39 y 37% respectivamente), seguida con la flora cosmopolita (27 y 37% respectivamente). La relativamente elevada participación florística cosmopolita sugiere un arribo reciente de esta flora.

The Sierra de La Laguna, located in Baja California Sur (the most arid state of all Mexico), has been considered an ecological island. Here, the lowlands consist of xeric vegetation, while the mountains and foothills harbor plant communities that are unique in all the peninsula of Baja California. A tropical deciduous forest is located in the foothills between 500 to 1000 m. In the mountains above 1000 m, woodland occupies an approximate surface of 300 to 350 km² and is composed of: a) an oak woodland between 1000 and 1500 m of elevation, dominated by the "roble" *Quercus tuberculata*; and b) the oak-pine woodland between 1500 and 2200 m, dominated by endemic species "pino piñonero" *Pinus cembroides* var. *lagunae*,

"encino negro" *Quercus devia,* "madroño" *Arbutus peninsularis,* and "sotol" *Nolina beldinguii.* This classification follows Rzedowski (1978), in accordance with Mexican nomenclature.

This paper is concerned with the woodland community, which is important not only in a biological sense, but because no other area of the state receives similar rainfall. Both the vegetation and soil allow the rain water to recharge the local aquifers, providing water for urban and suburban populations, ranches, tourist developments, and small agricultural areas.

Continued research consisting of field trips, bibliographical reviews, and consultation with both authorities and herbariums (UC, RSA, CAS, SD, and MEXU) has resulted in the addition of 48 taxa for the vascular flora. Previous publications (León de la Luz and Domínguez Cadena 1989; Breedlove and León de la Luz 1989) yielded 228 species and infraspecific taxa. The earliest collector in the Sierra, T. S. Brandegee (1891, and subsequent additions) cited no more than 200 taxa for approximately the same area.

Increased human settlement in the vicinity has resulted in the destruction of this natural resource, and thus the woodland is at risk of losing its natural balance. The main purpose of this study was to support the establishment of an ecological protected area by documenting the flora as a natural resource that needs to be preserved.

Materials and Methods

Study area. The Sierra de la Laguna is the highest range in the southern mountains of Baja California Sur, Mexico, with the highest peaks reaching 2200 m. It is crossed by the Tropic of Cancer at 109°58'W. This Sierra is comprised of six major canyons. Soils are sandy in texture, with a thin layer of top soil with organic matter; it is formed from decomposition of late cretaceous granitic rocks.

Foothills and adjacent low areas have a warm and dry climate, but climate in the woodland is rather cool, with light frosts occurring on winter nights. Much of the rain normally occurs in summer, though winter rains are often the heaviest. Total annual amount of rain ranges between 500 to 900 mm. The dry season is from late winter to early summer.

Methodology. Eleven seasonal visits were made to several sites in the area between 1987 to 1991. Almost seven hundred voucher specimens were prepared and housed at Centro de Investigaciones Biológicas de Baja California Sur Herbarium (HCIB). Species determinations were made or checked by comparison with corresponding ejemplars stored at California Academy of Sciences (CAS), San Diego Museum of Natural History (SD), and University of California Berkeley (UC) Herbariums, and by consultation with the following authorities: Dennis E. Breedlove (CAS), Allan Smith & Annetta M.

TABLE 1. NUMERICAL SYNOPSIS OF THE SIERRA DE LA LAGUNA FLORA. Table does not include two undetermined species and excludes three species, two of which are probably extinct (one of them a monospecific genus), and one which does not correspond to the flora but was cited in the previous catalogue. Endemics = 43 (38 species and 5 infralevel).

Life form	Number of species
Trees	17
Shrubs and subshrubs	30
Annual and perennial herbs	176
Hydrophites	34
Climbing	5
Succulents	8
Saprophites and parasites	2

Carter (UC), Shirley Graham (KEN), Thomas Philbrick and Dave Thompson (RSA), Warren L. Wagner (Smithsonian Institution), and Geoffrey Levin (SD). Some additions have been taken from bibliographic references (Gould and Moran 1981; Wiggins 1980; Johnson 1958). Nomenclature follows mainly to Wiggins (1980).

RESULTS

Plants communities. Because of floral and structural differences between some sites, presumably due to sun exposition, availability of water, soil depth, and other factors, the oak-pine community has been divided in four associations named: "Valleys", "Stream Bottoms", "True Woodland", and "Open Areas" (León de la Luz and Domínguez Cadena 1989).

The area occupied by the oak woodland or "encinar" is very precipitous, with step surfaces ranging from 30° to 40°. The vegetation consists of scattered trees (*Quercus tuberculata*), low shrubs (*Dodonaea viscosa*), and both annual and perennial herbs; where grasses are the physiognomic dominants (*Muhlenbergia emersleyi*). At the same altitudes, a local riparian plant association occupies the bottom of the brooks and canyons. Streams descend along the canyons to 700–600 m above sea level. This association is characterized by *Populus brandegeei* var. *glabra*, *Salix lasiolepis*, and the fan palms *Erythea brandegeei*, and *Washingtonia robusta*.

The current flora. Forty eight species of vascular plants have been added to the first catalogue (León de la Luz and Domínguez Cadena, 1989); four of these were re-identified, and 44 are new recordings. Sixteen annotated species (16/48) do not have voucher specimens. Table 1 enumerates the current flora of the woodland according to life forms. There are 272 species in 184 genera representing 69 families. Two additional species (*Solanum* aff. *fendleri* and *Anoda* sp.) are awaiting adequate identification or description, and were

TABLE 2. DISTRIBUTION OF THE 272 SPECIES OF VASCULAR PLANTS WHICH FORM THE RECOGNIZED FLORA OF THE WOODLAND COMMUNITIES OF THE SIERRA DE LA LAGUNA.

	Families	Genera	Species and infra categories
Pteridophytes	4	14	19
Gymnosperms	1	1	1
Angiosperms	64	169	252
Total	69	184	272

not considered in the table. Table 2 shows the distribution of all the species according to their taxonomy.

Annotated catalog. The catalog is included in Appendix I. Each entry includes information on life forms (cf. Table 1), habitat, occurrence, flowering phenology, and common name. Endemic species are marked with an asterisk (*). The most common synonyms are also included.

Rare species. Some of the T. S. Brandegee's collections which he reported as "unique" or "few" have not been found again; these were *Faxonia pusilla, Pectis uniaristata* var. *uniaristata, Muhlenbergia wolfii* and *M. ciliata.* Specimens of *Ilex californica* are very scarce, only a dozen living trees are known. Other rare species, numbering less than 20 in restricted locations include: *Aralia scopulorum, Arenaria lanuginosa* subsp. *saxosa, Ilex brandegeana, Myrtillocactus cochal, Quercus arizonica, Q. oblongifolia, Q. reticulata, Styrax argenteus,* and *Morangaya (Echinocereus) pensilis.*

Excluded species. Eriogonum inflatum var. *deflatum* (Polygonaceae) is reported by Wiggins (1980) but has been not collected by the authors; none of the *Eriogonum* species occur further south than the Vizcaino Desert, thus Wiggin's citation should be considered an error for this area.

Oxalis corniculata (Oxalidaceae), *Oenothera laciniata* subsp. *pubescens* (Onagraceae), *Quercus oblongifolia* (Fagaceae), and *Sisyrinchium bellum* (Iridaceae) were mistakenly identified, and their true identity is noted in the appendix A.

Faxonia pusilla may be considered an extinct species. Its description was based on only one specimen collected during the late 19th century, and it has never been collected since. The location of the type label (UC) is given as "Sierra de La Laguna", but it is possible that the collection was obtained somewhere in the tropical deciduous forest. *Echinochloa cruspavonis,* cited by Gould and Moran (1981) and known in a few of the 19th century collections, has not been collected recently. According to T. Philbrick (1990, personal communication), there is no reason to include *Podostemon ceratophyl-*

TABLE 3.   GEOGRAPHICAL AFFINITY OF FLORAL GROUPS OF FAMILIES AND GENERA OF THE VASCULAR FLORA OF SIERRA DE LA LAGUNA, AND THEIR NUMERIC CONTRIBUTION.

	Families Number (%)	Genera Number (%)
Tropical	28 (40.5)	109 (59.2)
Temperate	9 (13.1)	29 (15.7)
Cosmopolite	27 (39.2)	37 (20.1)
Disjointed	5 (7.2)	8 (4.4)
Endemic	0	1 (0.6)
Total	69	184

lum (Podostemonaceae) in this catalogue, our determination (cited in a previous work) was based on a sterile specimen of *Potamogeton.* The latter three species where not considered in our list.

Endemism. Before this work, a total of 228 species of vascular plants were reported for this region; thirty seven (37/228; 17%) species were considered endemic. The additions involve seven more endemic species. Two monospecific genera have been proposed as endemic, *Faxonia* (Compositae), and *Morangaya* (Cactaceae), but the former should be excluded because there is no evidence of its existence. Thus, the current number of endemic taxa is 43.

DISCUSSION

Some of the reports in the list of additions indicate range extensions of the correspondant taxa for the Sierra or the state. The incorporation of the additions did not modify the rate of endemisms; this remains at (43/272; 17%). The proportion of endemic species is moderate if compared to some of the closest natural areas such as Revillagigedo islands (32%), and Vizcaino Desert Biosphere Reserve (9%).

Table 3 shows the geographical affinity of the floral groups (families and genera) with the element tropical, temperate, cosmopolite (which includes worldwide, or pantropical), disjointed (some of the tropics, subtropics, or both tropic and temperate), and endemic. The corresponding family-genus with their geographical affinity was taken from Willis (1985). According to this same table, it is possible to observe that the tropical element is the most important at both the family and generic level, this result is not surprising because the Sierra always has been influenced by tropical climate since its geologic origin (Moore and Curray 1982). The temperate element only has moderate participation, the presence of these could be considered as remnants of the pleistocene flora, taxa of this category must be considered relictuals (Axelrod 1950, 1958).

Conclusions

The constant increase in the floral components in the Cape Region, where the Sierra is included, should not be attributed previous to incomplete field and identification work. It is possible that increasing human population and the trade traffic, has resulted in a continuous introduction of seeds over the last decades from mainland Mexico and several peninsular areas, many of them have achieved adapt to the conditions of this area and are now relatively common in landscape of certain communities (see Gilmartin and Neighbours 1978).

It has been said that the vegetation of the Cape Region has tropical features (Brandegee 1891; Shreve 1937; Wiggins 1960, and Rzedowski 1978); yet, the Sierra de la Laguna woodland does not appear to be distinct of this general pattern.

The relative low occurrence of endemisms in higher taxa (no families; and only two monospecific genera, one considered extinct and the other not well recognized), and moderate (17%) specific and infraspecific levels suggest that the isolation of the Sierra has not been effective. Rather, floristic incorporation from tropical and subtropical areas has resulted from a "continental bridge" with the west coast of mainland Mexico, or through certain areas of the Sonoran Desert. The authors are continuing to study the floristic composition of the Cape Region to answer the aforementioned questions.

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APPENDIX I.

ADDITIONS TO THE FLORA OF THE
SIERRA DE LA LAGUNA

The additions, with an asterisk (*), are endemic taxa.

Polypodiaceae

—*Pellaea ovata* (Desv.) Weatherby. Oak forest, rare, perennial herb. Sep.
—*Thelypteris rudis* (Kuntze) Proctor. Oak forest, hydrophyte. Aug.–Sep.

Graminae

—*Andropogon glomeratus* Walt. B.S.P. oak pine and oak woodland, perennial herb. Sep.–Nov.
—*Eragrostis pilosa* (L.) Beauv. Oak woodland, annual herb. Sep.–Dec.
—*Eragrostis orcuttiana* Vasey. Oak-pine forest, annual herb. No voucher.
—*Hackelochloa granularis* (L.) Kuntze. Oak forest, annual herb. No voucher.
—*Muhlenbergia alamosae* Vasey. Oak forest, perennial herb. No voucher.
—*Panicum sonorum* Beal. A relative common grass in Baja California, sporadic in the oak woodland. Sep.–Nov.
—*Peyritschia pringlei* (Scribn.) Koch. Oak pine forest. This genus has been revised by Koch & Hernández (CHAPA), integrating it in *Trisetum.* Annual. Sep.–Nov.
—*Vulpia microstachys* (Nutt.) Benth. var. *pauciflora* (Beal) Lonard & Gould. Oak pine and oak forest. No voucher.

Cyperaceae

—*Carex longissima* M. E. Jones. Oak forest, perennial herb. No voucher.

Iridaceae

—*Sisyrinchium bellum* S. Wats. Rare along shaded arroyos, perennial herb. Mar.–May. This is the true identity to *S. demisum* Greene, cited in the previous work. Jan.–July.

—*Sisyrinchium translucens* (Bicknell) S. Wats. Locally abundant in both shaded and open areas in the oak pine forest, annual herb. Sep.–Jan.

Orchidaceae

—*Habenaria crassicornis* Lindley. Perennial herb from rootstock. Rare in the oak pine woodland. Sep.
—*Habenaria novembifida* Lindley. Perennial herb along currents, rare in shaded arroyos. May.

Amaranthaceae

—*Alternanthera repens* (L.) Kuntze. Occurring in gravelly soils in disturbed areas, an introduced weed from the tropical zone, perennial herb, flower almost all the year.

Begoniaceae

—*Begonia californica* Brandegee. Perennial but acaulescent herb, locally abundant in the oak woodland beneath rocks along currents. Sep.

Boraginaceae

—*Heliotropium fallax* I. M. Jhtn. Uncommon weed in the oak woodland, locally abundant in the lowlands. Sep.–Nov.?.

Compositae

—*Bidens amphicarpa* Sherff. Annual herb, locally abundant along streams banks and shaded slopes. Sep.–Oct.
—*Bidens lemmoni* A. Gray. Annual herb, locally abundant in disturbed soils in the oak woodland. Sep.–Oct.
—*Bidens leptocephala* Sherff var. *hammerlyae* Sherff. Annual herb, locally abundant beneath oaks. Sep.–Oct.
—*Bidens tenuisecta* A. Gray. Annual herb, uncommon in open spaces among oaks. Sep.–Oct.
—*Galinsoga semicalva* St. John & White var. *percalva* S. F. Blake. Annual herb, infrequent beneath trees in the oak pine and oak woodland, flowers after summer rains.
—*Heterosperma coreocarpoides* (Sherff) Sherff. Cited by B. H. Johnson (Op. cit.). Perennial herb in exposed areas, both oak pine and oak woodland. Aug.–Dec.
—*Pectis urceollata* Rydb. Annual herb, cited by I. L. Wiggins (1980, Flora of Baja California, Stanford University Press) at elevations corresponding the tropical deciduous forest and oak woodland. No voucher.
—*Stevia rhombifolia* H.B.K.. Infrequent shrub in the oak woodland, flower after rains.
—*Tagetes subulata* Cerv. Annual herb, locally abundant in exposed areas in the oak woodland. Sep.

Crassulaceae

—*Tillaea aquatica* L. Hydrophyte, inhabits in pools and another quiet body waters, rare, first register for the state. Mar.–Jun.

Euphorbiaceae

—*Euphorbia apicata* L. C. Wheeler. Oak pine and oak woodland, uncommon, annual herb. No voucher.
—*Euphorbia dentosa* I. M. Jhtn. Rare annual in the oak woodland and other exposed areas. Aug.–Oct.

Fagaceae

—*Quercus albocincta* Trel. Small populations of this tree are located sparingly in the woodland. Flowers appear presumably in late spring. This is the true identity to *Q. oblongifolia* Torr. cited in the previous work.

Gentianaceae

—*Centaurium capense* Broome. It is the true identity of *C. nudicaule* (Engelm.) Robinson, cited in the previous paper. Little annual in the open areas in oak and oak pine woodland. Mar.–Apr.

Labiatae

—*Salvia marci* Epling. A little population of this shrub was found growing in rocks in the highest elevations of the Sierra. Oct.–Dec.

Leguminosae

—*Clitoria monticola* Brandegee. Subshrub locally abundant in rocky and shaded slopes. Aug.–Sep.
—*Desmodium neo-mexicanum* A. Gray. Annual herb, locally abundant at the edges of valleys, common in lowlands. Sep.–Nov.
—*Lotus scoparius* (Nutt. ex T. & G.) var. *brevialatus* Ottley. Perennial herb, valleys, locally abundant, Jul.–Dec. [=*Hosackia glabra* (Vogel) Torr. var. *brevialatus* (Ottley) Abrams.]. Sep.–Jan.
—*Senna goldmanii* (Rose) Irwin & Barnaby. Oak woodland, uncommon in arroyos. Shrub. Apr.–Jun.
—*Senna polyantha* (Colladon) Irwin & Barnaby. Infrequent shrub in the oak woodland, proper in the lowland. Aug.–Sep.
—*Stylosanthes viscosa* Swartz. Oak pine and oak woodland, locally abundant, perennial herb. Sep.–Mar.

Lythraceae

—*Cuphea micropetala* H.B.K. Rare hydrophyte, inhabits in arroyos in the oak woodland; Feb.–Mar.

Onagraceae

—*Jussiaea suffruticosa* L. var. *octofila* (DC.) Munz. Annual herb cited by B. H. Johnson. Aug.–Oct. No voucher.
—*Oenothera breedlovei* W. Dietrich & W. L. Wagner. Perennial herb, locally abundant in open areas and valleys in the oak pine woodland. Flower almost all the year. It is the correct identity of *O. laciniata* Hill. subsp. *pubecens* (Willd.) Raven. [=*O. pubescens* Willd. ex Spreng.] cited in the previous work.

Oxalidaceae

—*Oxalis corniculata* L. Habits open areas in the oak pine woodland, perennial herb. It is *O. albicans* H.B.K. cited in the previous work. Flowers almost all the year.

Rubiaceae

—*Houstonia asperuloides* (Bentham) A. Gray. Annual herb, locally abundant in sandy and exposed areas, relatively common at lowlands. Sep.–Feb.

Scrophulariaceae

—*Buchnera pusilla* H.B.K. Distributional record for this scarse and delicate sapro-phyte, known from tropical areas of mainland Mexico. Oct.

—*Galvezia juncea* (Benth.) Ball var. *pubecens* (Brandegee) I. M. Jhtn. Shrub growing in rock crevices, oak pine woodland. Sept.–Feb.

—*Mecardonia exilis* (Brandegee) Pennell. Hydrophyte, rare along arroyos, it is a species proper of the foothills of the range. Mar.–Apr.

—*Mimulus dentilobus* Rob. & Fernald. Hydrophyte, cited as uncommon along per-manent streams in the oak pine woodland (Wiggins 1980). No voucher.

Thymelaeaceae

—**Daphnopsis lagunae* Breedlove & León de la Luz. Shrub, locally abundant in open areas in both oak and oak pine woodland. Aug.

HYPERACCUMULATION OF NICKEL BY
ARENARIA RUBELLA (CARYOPHYLLACEAE)
FROM WASHINGTON STATE

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Abstract

The nickel concentration of whole plants of **Arenaria rubella** collected on dunite, Skagit County, Washington, U.S.A., is reported as 1360 μg g^{-1} (dry weight), compared with only 2.7 μg g^{-1} for specimens collected on shale, Jefferson County. This is the first hyperaccumulator of nickel reported from northwestern North America. High concentrations of chromium, cobalt and iron at 213, 33.5 and 28,900 μg g^{-1}, respectively, in plants from dunite contrast with low values (3, 0.49 and 600 μg g^{-1}) in samples from shale.

During the past 20 years many taxa, mostly endemic to the nickel-rich soils derived from ultramafic outcrops, have been reported as accumulating nickel in high concentrations (Brooks et al. 1977; Peterson 1983; Brooks 1987). Such plants have been termed "hyperaccumulators" when containing >1000 μg g^{-1} Ni (dry weight) (Brooks et al. 1977). The term, hyperaccumulator, should not be thought to infer a physiological or biochemical basis for high values of metal uptake. Rather, it simply serves to indicate unusually high concentrations in plant tissues. Hyperaccumulator plants, then, exemplify one specialized consequence of living in a heavy metal environment.

The numerous reports from several countries on metal concentrations in plants from ultramafic soils have been based primarily on samples from herbarium specimens. Thus, the first hyperaccumulator of nickel in North America, *Streptanthus polygaloides* Gray, with 9750 μg g^{-1}, was detected in this manner (Reeves et al. 1981, 1983). We report here an instance of hyperaccumulation of nickel based on field-collected samples. We found *Arenaria rubella* (Wahlenb.) J. E. Smith to be the only hyperaccumulator in tests of 42 species of flowering plants, conifers and ferns collected on ultramafics in Washington state. Appendix 1 lists those plants found not to be hyperaccumulators.

Materials and Methods

Samples of whole plants were collected at two sites on ultramafic rock and one on shale. The *Arenaria rubella* samples of ultramafics came from a large dunite deposit (the Twin Sisters dunite) at the Olivine Bridge Natural Area, South Fork Nooksack River, Skagit County, elevation 540 m (1900 ft). Dunite is an ultramafic igneous rock consisting of the iron-magnesium silicate mineral, olivine; nickel and chromium are commonly found in dunite. Soils derived from dunite and serpentinite are azonal (skeletal), shallow and with no profile development. Two samples of soil (Kruckeberg nos. 6660 and 6662) were collected for chemical analysis (Table 2). The soils were air-dried and separated into 2 mm and coarse fractions. Replicate samples were analyzed for nickel, chromium, cobalt, iron, magnesium and calcium by atomic absorption spectrophotometry using the techniques described below for tissues; less than 2 mg of each sample was used in each determination.

The dunite conglomerate at Olivine Bridge supports a sparse stand of stunted conifers: *Pseudotsuga menziesii* (Douglas fir), *Pinus contorta* (lodgepole pine), *P. monticola* (western white pine) and *Juniperus communis* (common juniper). On intervening barren areas only a few widely spaced herbs grow: *Arenaria rubella, Cerastium arvense, Aspidotis densa* and *Achillea millefolium* (Kruckeberg 1969). Nearby non-ultramafic sites support typical second-growth mixed conifer-hardwood stands. The samples were taken on 22 September 1980 and on 27 July 1981.

The *Arenaria rubella* samples from a shale outcrop were collected on 22 August, 1981 at Buckhorn Pass at 1500 m (5000 ft) in the northeastern sector of the Olympic Mountains, Jefferson County, Washington, in a subalpine fellfield. This locality is in the midst of an *Abies lasiocarpa* (subalpine fir)-parkland habitat with a rich grass/forb cover.

Samples of *Arenaria obtusiloba* (Rydb.) Fern. were taken on 4 September 1980 on serpentinized peridotite along Eldorado Creek, upper North Fork Teanaway River, Kittitas County. The site is in an open, mixed conifer forest with Douglas fir, lodgepole pine, western white pine, *Pinus ponderosa* (yellow pine), *P. albicaulis* (whitebark pine) and common juniper (Kruckeberg 1969). *Arenaria obtusiloba* grew on barren talus and on ridges as widely scattered individuals. It occurs with *Aspidotis densa, Douglasia nivalis* var. *dentata, Polystichum lemmonii, Poa curtifolia, Lomatium cuspidatum* and *Chaenactis thompsonii*; the latter four species are serpentine endemics in the Wenatchee Mountains (Kruckeberg 1969).

Ten individuals were collected at each of the four sites, including two different dunite locations at Olivine Bridge. Entire rosettes of separate but neighboring individuals were chosen at a given site.

Whole-plant samples (roots and shoots) were prepared for analysis by washing in distilled water and drying to constant weight at 70°C. The whole plants were powdered in a commercial (Braun) mill and 2 g subsamples were dry ashed at 450°C until all traces of organic matter had disappeared. The ash was leached with hot 2 M HCl and diluted to 10 ml. Samples were analyzed for nickel, chromium, cobalt, iron, magnesium and calcium by atomic absorption spectrophotometry using a Varian Techtron Mark 5 flame atomic absorption spectrophotometer. Nickel analyses were performed at a wavelength of 231.7 nm with an air-acetylene mixture and oxidizing flame stoichiometry (Shewry and Peterson 1976).

Results and Discussion

The analytical data for *Arenaria rubella* collected from an ultramafic and a nonultramafic site are presented in Table 1 together with data for *A. obtusiloba*. Higher concentrations of nickel, chromium, cobalt, iron and magnesium and lower concentrations of calcium occur in plants from the dunite outcrop compared with those collected on shale. The high nickel concentration in *A. rubella* puts it in the hyperaccumulator category.

The nickel concentration in *A. rubella* (1360 μg g^{-1}) on dunite is approximately one half the total soil nickel concentration of 2643 μg g^{-1} (dry weight; Table 2). When expressed on an ash weight basis, plant nickel concentration greatly exceeds soil nickel. On a dry weight basis, the 5260 μg g^{-1} calcium concentration in plants exceeds the soil concentration of 1944 μg g^{-1} indicating that soil contamination is unlikely to be a significant source of analytical error. The Ca:Mg ratio for *A. rubella* of 0.08 lies within the range of values recorded for other species on serpentine soils (Shewry and Peterson 1976).

Although *A. rubella* is a widely distributed circumpolar species, it seems likely that the specimens collected from the dunite site are from a serpentine race, physiologically but not morphologically, different from the non-serpentine race. *Arenaria rubella* is known from ultramafic sites on the Gaspé Peninsula of eastern Canada (Rune 1954) and from Scandinavia (Rune 1953); no data on nickel accumulation for these occurrences are available. *Arenaria obtusiloba* is another widespread sandwort, ranging from Alaska across North America to the Gaspé and Greenland. Though it is not wholly restricted to ultramafics, it is a highly faithful indicator of ultramafics in the Wenatchee Mountains (Kruckeberg 1969), the source of the present samples.

Preliminary reports of Roberts (1979, 1980) have indicated that two other species of *Arenaria, A. humifusa* Wahlenb. and *A. marcesens* Fern. from a serpentine area in western Newfoundland, Canada, can also be classified as hyperaccumulators, with nickel con-

TABLE 1. METAL CONCENTRATIONS IN WHOLE PLANTS OF *ARENARIA RUBELLA* AND *A. OBTUSILOBA* COLLECTED IN WASHINGTON STATE.

Species	Locality	Rock type	n	Ni	Cr	Co	Fe	Mg	Ca
						(μg g^{-1} dry weight)			
A. rubella	Skagit County	Dunite	3	1360.0	213.0	33.5	28,900	63,700	5260
A. rubella	Jefferson County	Shale	1	2.7	3.0	0.5	600	1480	19,000
A. obtusiloba	Kittitas County	Peridotite	1	104.0	15.7	6.4	1220	14,600	13,500

TABLE 2. ANALYSIS OF TWO DUNITE SOILS, OLIVINE BRIDGE AREA, SKAGIT COUNTY, WASHINGTON.

Collection number	Ni	Cr	Co	Mg	Fe	Ca
			(μg/g of dry weight soil)			
Olivine Bridge						
6660	1393	266	82.7	48,120	92,054	2629
Standard deviation	38.3	40.0	3.27	1161	1394	136
Coefficient of variation (%)	(2.75)	(15.0)	(3.95)	(2.41)	(1.51)	(5.18)
6662	2643	98.0	77.6	59,741	66,638	1944
Standard deviation	90.2	17.1	3.00	1951	1378	471
Coefficient of variation (%)	(3.41)	(17.4)	(3.86)	(3.27)	(2.07)	(24.2)

centrations of 2330 and 2365 μg g^{-1} (dry weight), respectively. The absence of hyperaccumulation in *A. obtusiloba* in the present study, however, reveals that this phenomenon does not occur in all members of the genus. Other *Arenaria* species are found on serpentine locations in Scandinavia (Rune 1953). Although not hyperaccumulators of nickel, they are likely to be adapted physiologically to the nickel-rich substrates by either accumulating or excluding nickel (Shaw 1989).

Data on nickel hyperaccumulators from various sources worldwide suggest a taxonomic bias at the genus and family level. Hyperaccumulators are found in the mustard family, Brassicaceae (Cruciferae), with exceptional frequency (Brooks 1987; Reeves et al. 1981, 1983; Roberts 1980). Although nickel-tolerant and nickel-accumulating races of *Silene, Cerastium* and *Arenaria (Minuartia)* have been reported within the Caryophyllaceae, these races have not to date been recorded as hyperaccumulators. As more chemical data on them become available, correlations between taxonomic groupings and affinity for heavy metals are likely to emerge. Such is the case for *Alyssum* (Brassicaceae) in which some 14 species found on European serpentine soils are hyperaccumulators of nickel (Brooks and Radford 1978). Clearly, examination of the various physiological mechanisms permitting hyperaccumulation is required to understand this presumed adaptive phenomenon. This sequestering of accumulated heavy metals is one way plants may avoid the toxic effects of the element (Baker and Walker 1989).

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APPENDIX I.

OTHER COLLECTIONS ANALYZED FOR HEAVY METAL ACCUMULATION

None were hyperaccumulators of nickel. Data available from first author (ARK).

Skagit Co., Washington

A. Olivine Bridge area, South Fork Nooksack River, ultramafic (dunite) soil: *Pteridium aquilinum, Achillea millefolium, Elymus glaucus, Adiantum aleuticum, Aspidotis densa, Silene paradoxa* (introduced "founder" population), *Carduus acanthoides* (weed), *Cerastium arvense, Silene menziesii, Prunella vulgaris* (introduced), *Fragaria virginiana* var. *crinita, Pseudotsuga menziesii, Juniperus communis, Pinus contorta, Gaultheria shallon, Alnus rubra, Spiraea menziesii, Ledum groenlandicum, Menziesia ferruginea.*

B. West of Olivine Bridge, non-ultramafic soil (mostly on argillite): *Adiantum aleuticum, Pteridium aquilinum, Pseudotsuga menziesii.*

C. Fidalgo Head, 5 miles west of Anacortes, on ultramafic soil (alpine peridotite): *Juniperus scopulorum, Arbutus menziesii, Aspidotis densa.*

Kittitas Co., Washington

A. Eldorado Creek area, upper North Fork Teanaway River, ultramafic (serpentinized peridotite) soil: *Adiantum aleuticum* (I), *Aspidotis densa* (I), *Polystichum lemmonii* (E), *Chaenactis thompsonii* (E), *Anemone drummondii* (I), *Douglasia dentata nivalis* (I), *Lomatium cuspidatum* (E), *Poa curtifollia* (E), *Eriogonum pyrolaefolium coryphaeum* (I), *Silene parryi, Achillea millefolium lanulosa, Pseudotsuga menziesii, Pinus contorta, P. ponderosa, Juniperus communis, Pinus albicaulis, Abies lasiocarpa, Taxus brevifolia, Ledum columbianum, Salix brachycarpa* (I).

B. Below Eldorado Creek area, non-ultramafic soils: *Pseudotsuga menziesii, Pinus ponderosa.*

E = ultramafic endemic; I = indicator of ultramafics, but non restricted thereto.

EFFECTS OF TIMBER HARVEST TREATMENTS ON UNDERSTORY PLANTS AND HERBIVORES IN NORTHEASTERN CALIFORNIA AFTER 40 YEARS

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Abstract

Effects of five timber harvest treatments were evaluated in a pine forest after 40 years. Trends are presented for plant cover, frequency, density, and biomass, as well as on use by three herbivores. Tree growth, mortality, and high natural variability reduced differences among treatments over time. Strongest correlations of understory biomass were with litter, tree dominance, and elevation.

Timber harvesting is widespread in the Pacific Northwest, yet data are lacking on the long-term (>20 years) effects of different timber harvest methods on understory vegetation and subsequent use by herbivores. The purpose of this study was to evaluate the vegetation recovery 40 years after logging in a pine forest in northeastern California.

Methods

The study area was in Blacks Mtn Experimental Forest, Lassen Co. Approximately half of the study area is in a gently rolling basin; the rest extends up moderate slopes to the north and east. Elevations vary from 1700 to 2100 m. Forest vegetation is characteristic of the Interior Ponderosa Pine type (Eyre 1980) and descriptions specific to the study area are provided in Hallin (1959) and Vora (1988a). Timber volumes (trees larger than 29.5 cm diameter at 1.4 m) were about 105,000 to 116,500 m³/ha prior to logging (Hallin 1959).

Effects of timber harvest were measured within blocks subjected to six treatments: control (no cutting), 3 levels of partial cutting (removal of 15%, 55% and 75% of timber volume designated as light, moderate, and heavy partial cuts), removal of small groups of trees 29.5 cm diameter and greater (diameter limit cut, about 95% of timber volume), and light partial cutting followed by removal of small groups of trees 10 years later (group selection). The light partial cut consisted of removal of insect-damaged trees. A total of about 30% of the original timber volume was removed in the group selection treatment over a 10 year period (1949–1957). A randomized

block design was used and 4 to 6 treatments were allocated randomly to 8 ha units within each of 5 blocks. These treatments were initiated 40 years ago for a study of tree growth (Hallin 1959). There were no post-harvest treatments and all regrowth was natural.

To estimate treatment effects, 10 plots were randomly placed along a transect in each treatment unit and the tree density (100 m² plots), tree cover and frequency (25 m²), shrub biomass (9.3 m²), herbaceous biomass (0.84 m²), and litter-duff-ground layers were measured as well as droppings of mule deer (*Odocoileus hemionus*), snowshoe hare (*Lepus americana*), and cattle (25 m²) (Vora 1986, 1988a, b, c). All field work was completed between June of 1983 and August of 1984. Plant nomenclature is according to Munz (1973). Data analyses methods included analyses of variance, multiple comparison tests, correlations, principal components analyses, and stepwise regression (Statistical Analysis System 1982).

RESULTS AND DISCUSSION

Effects on vegetation. Comparisons of effects of timber harvest methods show some trends (Table 1). The density of large trees was higher in the uncut control. Tree basal area, total tree density, and density of small trees were higher in the control and light partial cut. Pole-sized trees were less common in the control. Emphasis on removal of *C. decurrens* in cutting prescriptions (Dunning and Hasel 1938) was probably the reason for significantly more of that species in the control plots. The fewer *Pinus* species trees in the heavier cuts was probably due to replacement by more shade-tolerant *A. concolor*. Reduced fire frequency caused by fire suppression probably helped establishment and survival of *A. concolor* seedlings (Agee et al. 1978).

More snags were observed in the control and lightly cut treatments (light and moderate partial cuts, and group selection). Perhaps, differences among treatments in cavity-nesting birds could be detected.

More small trees were expected in the heavier timber cuts. Instead, more seedlings and saplings were found in the control and light partial cut stands. Treatment means for age of saplings (2.5 to 14.2 cm dbh) were remarkably similar, 48 to 53 years (range of 33 to 100 years). This did not vary with either species or tree diameter. This finding supports the observation by Gordon (1967) that nearly all the young growth on Blacks Mountain pre-dated the original timber harvest treatments (Gordon's estimate of 90 years is much higher than my measured mean of 48 to 53 years). Gordon (1967) suggested that most of the understory probably originated soon after sheep stopped grazing the land and left a good seedbed. Dunston and Wieslander (1933), in their establishment report on the Blacks Mountain Experimental Forest, reported that it was then grazed by 50 head of cattle and 1200 head of sheep between 1 June and 30

September, and the range condition was "good." Conditions after the 1939–1952 timber harvests were apparently not as favorable for natural tree regeneration; seed availability, climatic factors, biotic factors (seed-eating rodents), ground cover, competition by other vegetation (Roy 1983), and possibly soil compaction in skid trails (Vora 1988d) may have combined to be limiting.

Bareground cover and fuel loadings of all size classes were lower in the control and light partial cut. Litter volume estimates were higher in those treatments.

Non-random distribution of understory vegetation and only 3 replications of the light partial cut and diameter-limit cut made trends in variables measuring understory vegetation shown in Table 1 difficult to interpret. Frequencies of *Viola purpurea, Gayophytum humile,* and *Collinsia torreyi* were higher in the heavier cuts (moderate and heavy partial cuts, diameter-limit cut) (Vora 1988a). The frequency of grasses (family Poaceae as a group) was lower in the control and lighter cuts (light partial cuts and group selection).

Overstory, litter, and environmental variables correlated with shrub, twig, forb, and grass biomass (Table 1). The strongest correlations ($P < 0.001$) with understory biomass were litter, total tree cover, bareground cover, total tree density, number of small trees (2.5 to 27.7 cm dbh), *Abies concolor* dominance (canopy cover, densities by size classes, basal area), and elevation. Principal Components Analyses did not contribute to data reduction for the purpose of determining overstory-understory relationships. When run with 21 variables, for example, sixteen components were needed to describe 95% of the variance. Litter cover or volume was usually the first term in descriptive equations predicting understory biomass derived by stepwise regression. These equations, derived under the assumption of cause and effect (Ffolliot and Clary 1972 and others), explained 14 to 48% of the variance in microplots and 50–96% of the variance in treatment unit means (Vora 1986).

Tree growth and high insect-caused mortality (Hallin 1959; Hart 1983) reduced differences in treatment effects on understory over time. Gap openings in old-growth control stands caused by insect mortality and, formerly, natural fire, created a mosaic of small, even-aged clumps of trees of a variety of age classes. Such natural heterogeneity probably existed 40 years ago when treatments were applied, thereby making determination of treatment effects difficult. Results were statistically non-significant ($P > 0.05$) because of high variability and small sample sizes (5 blocks or replications).

Effects on herbivores. Snowshoe hare droppings were correlated positively with litter and tree variables, negatively with bareground cover, but not with any variables measuring understory biomass. Snowshoe hares prefer dense forests (Bittner and Rongstad 1982).

TABLE 1. COMPARISON OF EFFECTS OF TIMBER HARVEST METHODS AFTER 40 YEARS. [1] Numbers followed by the same or no letter were not significantly different (P < 0.05). [2] Measured with a spherical densiometer. [3] Nonparametric ANOVA. [4] ln transformation.

Variable	Treatment						ANOVA (P)
	Light partial cut (15%)			Moderate partial cut (55%)	Heavy partial cut (75%)	Cut >29.5 cm diameter	
	Control (No cutting)	No further treatment	Trees removed 10 yr later				
Trees							
Tree canopy cover (%)[2]	55	57	43	45	50	51	0.48
Tree basal area (m³ ha)	27	29	20	21	22	18	0.09
Total trees per ha	2802	3020	2090	1772	2522	1730	0.64[3]
Large trees per ha (>63.4 cm dbh)	34	14	4	14	14	8	0.01[1]
Pole trees per ha (14.3–27.7 cm dbh)	214c	454ab	284abc	244bc	388ab	304abc	0.05
Small trees per ha (2.5–14.2 cm dbh)	2484	2396	1684	1430	2043	1243	0.09[3]
Pinus spp. trees per ha	1878	1920	1348	1166	1308	533	0.83
Calocedrus decurrens trees per ha	460	173	196	158	254	170	0.06[3]
C. decurrens canopy cover (%)	7a	1b	2b	2b	4ab	1b	0.04
Abies concolor trees per ha	464	913	546	448	960	1013	0.12
Ground							
Total fuels (tonne/ha)	16ab	7b	28a	28a	26a	31a	0.02[3]
Litter volume (m³ ha)	272a	336a	176ab	100b	212a	164ab	0.05[4]
Bareground cover (%)	2b	<1b	6ab	6ab	4b	10a	0.05
Shrubs							
Ceanothus prostratus frequency (%)	68a	70a	78a	68a	54ab	17b	0.02
C. prostratus cover (%)	16	18	17	17	13	2	0.20
Arctostaphylos patula frequency (%)	26b	28ab	52a	40ab	34ab	18b	0.02
A. patula biomass (kg/ha)	253	6	411	141	184	10	0.10
Purshia tridentata (kg/ha)	252	243	181	237	215	571	0.60
Artemisia tridentata (kg/ha)	<1	<1	96	95	151	732	0.38

TABLE 1. CONTINUED.

| | | Treatment | | | | | |
| | | Light partial cut (15%) | | | | | |
Variable	Control (No cutting)	No further treatment	Trees removed 10 yr later	Moderate partial cut (55%)	Heavy partial cut (75%)	Cut >29.5 cm diameter	ANOVA (P)
Forbs							
Viola purpurea frequency (%)	16	16	12	24	24	20	0.25
Gayophytum humile frequency (%)	6	0	8	14	10	33	0.03
Collinsia torreyi frequency (%)	18	13	30	32	30	40	0.49
Grasses							
Family Poaceae frequency (%)	70	76	76	89	92	94	0.14
Herbivores (cumulative droppings per ha)							
Deer	168ab	107b	216ab	160ab	104b	280a	0.02
Recent deer (Summer 1983)	8	13	24	8	8	13	0.81
Snowshoe hare	448	506	376	136	280	320	0.51
Cow	48	65	24	80	16	92	0.62

Mule deer populations were too low to allow analysis of effects of treatments, and the 8-ha treatment units were probably too small. Frequency of droppings in 25-m² subplots was 20% for mule deer, 35% for snowshoe hare, and 10% for cattle. Animal presence was probably also influenced by factors such as water, predation, and disturbance that were not controlled in this experiment. Both deer and cattle were most common in the vicinity of sagebrush meadows and water. Cattle were not found at higher elevations. *Purshia tridentata,* a favored browse species (Leach 1952) was common at the lower elevation meadow edges (Vora 1988a).

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ANNOUNCEMENT

THE 1992 JESSE M. GREENMAN AWARD

The 1992 Jesse M. Greenman Award has been won by Sharon Elaine Bartholomew-Began for her publication "A morphogenetic re-evaluation of *Haplomitrium* Nees (Hepatophyta)", published as Volume 41 of Bryophytarum Bibliotheca. This study is based on a Ph.D. dissertation from Southern Illinois University at Carbondale, under the direction of Dr. Barbara Crandall-Stotler.

The Greenman Award, a certificate and a cash prize of $500 is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1992 are now being accepted for the 25th annual award, which will be presented in the summer of 1993. Reprints of such papers should be sent to Dr. P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, USA. In order to be considered for the 1993 award, reprints must be received by 1 June 1993.

HYMENOXYS JAMESII (ASTERACEAE: HELIANTHEAE): A NEW SPECIES FROM ARIZONA

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Abstract

Hymenoxys jamesii is a new species endemic to the Mogollon Plateau of Arizona. Morphologic, cytologic, and chemical data are all consistent with its recognition as a species in *Hymenoxys* subgenus *Picradenia,* where it appears to be most similar to the more widespread *H. cooperi.*

Resumen

Se describe una nueva especie endémica, **Hymenoxys jamesii,** del Altiplano Mogollon de Arizona. Datos morfológicos, citológicos y químicos son consistentes con reconocimiento de este taxón como una especie de *Hymenoxys* subgénero *Picradenia,* adonde se parece mas a *H. cooperi,* un taxón de ambito geographico amplio.

For several years I have collected plants of the genus *Hymenoxys* on the Mogollon Plateau of eastern central Arizona. It appeared that these plants were closely related to but distinct from plants classified as *Hymenoxys cooperi* (A. Gray) Cockerell; however, caution was warranted until type studies could be done because *H. cooperi* is widespread and morphologically very variable and several variants had already been described as species or varieties. Now that I have completed type, morphologic, and cytologic studies, I am confident that this entity has not been described previously and that it should be recognized as a species in *Hymenoxys* subgenus *Picradenia.*

Materials and Methods

Type specimens were borrowed from BM, F, GH, K, MICH, MO, NDG, PH, RM, NY, UC, and US.

For morphologic studies, representative specimens from throughout the ranges of *Hymenoxys jamesii* and *H. cooperi* (see Fig. 1) were examined for descriptive purposes and for counts and measurements dealing with plant height, stem number, midstem leaf width, peduncle length, head number, height, and diameter, and receptacle height and diameter. For counts and measurements dealing with outer and inner involucral bract number, length, and width, ligule number, length, and width, disc corolla length and diameter, disc corolla tube length, achene length and diameter, pappus scale number, length, and width, and pappus scale awn length, nine spec-

imens of *H. jamesii* and 11 specimens of *H. cooperi* (each from a different population) from throughout the range of each taxon were selected, and one or two flowering heads were removed from each for examination. The heads were dissected after they had soaked in detergent water, and all parts except for the ligules were allowed to dry before any measurements were made. From each head, all of the involucral bracts and ligules were counted and measured, ten disc corollas were selected for measurements, ten achenes were selected for measurements and for pappus scale counts, and one pappus scale from each achene was selected for measurements. Counts and measurements are presented in the description as the mean plus or minus one standard deviation followed by the range (given as minimum to maximum) and sample size (n). Characters from the different taxa were compared using the unpaired, two-tail t-test (Table 1). Because separate t-tests were run on multiple characters, a difference is not considered to be statistically significant unless $P \leq 0.01$. All statistical work was done with StatView® 512+ (Abacus Concepts, 1986) on a Macintosh II computer.

For cytologic studies, bud material was fixed in a modified Carnoy's solution: chloroform, absolute ethanol, and glacial acetic acid (4:3:1; V:V:V). Chromosomes were stained with acetocarmine, and counts were obtained from microsporocytes at metaphase I. The voucher specimen is deposited at TEX.

RESULTS AND DISCUSSION

Taxa included in *Hymenoxys* subgenus *Picradenia* are biennials or perennials of North America. They have involucral bracts that are arranged in two morphologically distinct series; the inner bracts are free, and the outer bracts are united for some portion of their length. As recognized here, subgenus *Picradenia* contains 11 taxa: *H. brachyactis* Wooton & Standley, *H. cooperi* (A. Gray) Cockerell, *H. helenioides* (Rydb.) Cockerell, *H. jamesii* Bierner, *H. lemmonii* (E. Greene) Cockerell, *H. quinquesquamata* Rydb., *H. richardsonii* (Hook.) Cockerell var. *richardsonii, H. richardsonii* var. *floribunda* (A. Gray) K. Parker, *H. rusbyi* (A. Gray) Cockerell, *H. subintegra* Cockerell, and *H. vaseyi* (A. Gray) Cockerell. Other taxa commonly included in *Hymenoxys* are here recognized as belonging to other subgenera of *Hymenoxys* or to separate genera.

All original descriptions and type specimens referable to *Hymenoxys* subgenus *Picradenia* were examined, and none of them matched the Arizona plants treated here as *Hymenoxys jamesii*. Furthermore, I am now of the opinion that *H. cooperi* is but one taxon and that the following names (along with their associated nomenclatural synonyms) should be treated as taxonomically synonymous with *H. cooperi*: *Actinella richardsonii* (Hook.) Nutt. var. *canescens* D. Eaton

TABLE 1. COMPARISON OF *HYMENOXYS JAMESII* AND *H. COOPERI*. For characters compared by t-test, the unpaired t value (t) and two-tail probability (P) are shown following the character. Counts and measurements are presented as the mean plus or minus one standard deviation followed by the sample size (n).

Character	Characteristic	
	H. jamesii	*H. cooperi*
Flowering date	summer	spring
Habit	apparently biennial	apparently biennial
Plant height (t = 2.56; P = 0.0141)	6.0 ± 1.7 dm (n = 28)	4.8 ± 1.4 dm (n = 18)
Number of stems from the base	usually 1	usually 1
Stem branching pattern	paniculate to corymbose	paniculate to corymbose
Stem pubescence	sparse to dense	sparse to dense
Stem coloration	usually purple-red below	usually purple-red below
Basal leaf segment number	(3–)5–7(–9)	3–5(–7)
Basal leaf pubescence	usually sparse	moderate to dense
Lower leaf segment number	3–5(–7)	3–5(–7–9)
Lower leaf pubescence	sparse to moderate	sparse to usually moderate
Middle leaf segment number	3–5	3–5
Middle leaf pubescence	sparse to dense	sparse to dense
Upper leaf segment number	1–3(–5)	1–3
Upper leaf pubescence	sparse to dense	sparse to moderate
Midstem leaf width (t = –2.26; P = 0.0262)	1.4 ± 0.3 mm (n = 61)	1.6 ± 0.4 mm (n = 25)
Peduncle apex pubescence	moderate to dense	moderate to dense
Peduncle length (t = –9.23; P = 0.0001)	2.6 ± 1.0 cm (n = 56)	5.6 ± 2.1 cm (n = 44)
Head number (t = 5.38; P = 0.0001)	114 ± 65 per plant (n = 28)	25 ± 18 per plant (n = 16)
Head shape	subhemispheric to campanulate	subhemispheric to hemispheric
Head height (t = –19.72; P = 0.0001)	5.9 ± 0.7 mm (n = 59)	9.1 ± 0.8 mm (n = 37)
Head diameter (t = –23.94; P = 0.0001)	6.4 ± 1.0 mm (n = 59)	12.8 ± 1.6 mm (n = 37)
Receptacle shape	hemispheric to usually conic	hemispheric to usually conic
Receptacle height (t = –8.28; P = 0.0001)	1.3 ± 0.3 mm (n = 20)	2.3 ± 0.4 mm (n = 20)
Receptacle diameter (t = –11.642; P = 0.0001)	1.7 ± 0.4 mm (n = 20)	3.8 ± 0.7 (n = 20)
Outer bract number (t = –7.45; P = 0.0001)	8 ± 1 per head (n = 18)	12 ± 2 per head (n = 11)

TABLE 1. CONTINUED.

Character	Characteristic	
	H. jamesii	*H. cooperi*
Outer bract shape	ovate to lanceolate	lanceolate
Outer bract outer surface pubescence	sparse to moderate	sparse to dense
Outer bract length (t = −26.47; P = 0.0001)	3.5 ± 0.5 mm (n = 86)	6.6 ± 1.0 mm (n = 135)
Outer bract width (t = −12.87; P = 0.0001)	1.2 ± 0.3 mm (n = 86)	1.8 ± 0.4 mm (n = 136)
Inner bract number (t = −7.91; P = 0.0001)	10 ± 2 (n = 18)	17 ± 3 (n = 11)
Inner bract shape	obovate	obovate to narrowly obovate
Inner bract outer surface pubescence	glabrous to moderate	sparse to moderate
Inner bract length (t = −31.26; P = 0.0001)	3.4 ± 0.4 mm (n = 111)	5.4 ± 0.6 mm (n = 184)
Inner bract width (t = −12.31; P = 0.0001)	1.6 ± 0.3 mm (n = 111)	2.1 ± 0.4 mm (n = 184)
Ray floret number (t = −9.40; P = 0.0001)	8 ± 1 (n = 18)	12 ± 2 (n = 11)
Ligule upper surface pubescence	glabrous	glabrous
Ligule lower surface pubescence	sparse	sparse
Ligule length (t = −35.09; P = 0.0001)	6.5 ± 0.9 mm (n = 142)	14.3 ± 2.5 mm (n = 128)
Ligule width (t = −23.46; P = 0.0001)	3.3 ± 0.6 mm (n = 141)	6.1 ± 1.3 mm (n = 128)
Disc corolla pubescence	glabrous to dense	moderate
Disc corolla length (t = −18.14; P = 0.0001)	2.6 ± 0.2 mm (n = 90)	3.6 ± 0.5 mm (n = 110)
Disc corolla diameter (t = −3.91; P = 0.0001)	0.5 ± 0.1 mm (n = 90)	0.6 ± 0.1 mm (n = 110)
Disc corolla tube length (t = −14.2; P = 0.0001)	0.7 ± 0.1 mm (n = 90)	1.1 ± 0.2 mm (n = 110)
Achene shape	narrowly obconic	narrowly obconic
Achene pubescence	dense	dense
Achene length (t = −14.88; P = 0.0001)	1.9 ± 0.1 mm (n = 90)	2.6 ± 0.5 mm (n = 110)
Achene diameter (t = −14.17; P = 0.0001)	0.5 ± 0.1 mm (n = 90)	0.8 ± 0.2 mm (n = 110)
Pappus scale number (t = −3.79; P = 0.0002)	usually 5 per achene (n = 115)	5 ± 1 per achene (n = 110)
Pappus scale shape	obovate	obovate
Pappus scale length (t = −23.02; P = 0.0001)	1.3 ± 0.3 mm (n = 115)	2.6 ± 0.4 (n = 110)
Pappus scale width (t = −9.63; P = 0.0001)	0.8 ± 0.1 mm (n = 115)	1.0 ± 0.2 mm (n = 110)
Pappus awn length (t = −6.89; P = 0.0001)	0.2 ± 0.1 mm (n = 26)	0.4 ± 0.1 mm (n = 75)

in S. Watson, *Actinella biennis* A. Gray, *Hymenoxys canescens* (D. Eaton) Cockerell var. *nevadensis* Cockerell, *Hymenoxys cooperi* (A. Gray) Cockerell var. *argyrea* Cockerell, and *Hymenoxys virgata* Nelson.

Hymenoxys jamesii differs from *H. cooperi* in many of its characters (Table 1). Most notably, the two taxa differ with regard to flowering date, and they are statistically significantly different from one another in peduncle length, number of heads per plant, head height and diameter, receptacle height and diameter, outer and inner bract number, length, and width, ray floret number, ligule length and width, disc corolla length and diameter, disc corolla tube length, achene length and diameter, pappus scale number, length, and width, and pappus awn length. Of these, the most useful characters for diagnostic purposes are flowering date, number of heads per plant, head height and diameter, outer and inner bract number, ray floret number, and ligule length and width.

Conversely, *Hymenoxys jamesii* and *H. cooperi* are very similar with regard to habit, stem and leaf characteristics, ligule pubescence, achene shape and pubescence, and pappus scale shape (Table 1).

Hymenoxys cooperi and several other taxa in *Hymenoxys* subgenus *Picradenia* (*H. helenioides, H. quinquesquamata, H. richardsonii* var. *richardsonii* and *H. richardsonii* var. *floribunda, H. rusbyi, H. subintegra,* and *H. vaseyi*) have all been reported to have chromosome numbers of $n=15$ (Speese and Baldwin 1952; Strother 1966; Kovanda 1972; Watson 1973; Keil & Stuessy 1975; Hartman 1977). The only suggestion of dysploidy in subgenus *Picradenia* comes from one report of $n=14$ for *H. richardsonii* (presumably var. *richardsonii*) from Canada (Taylor & Brockman 1966). *Hymenoxys jamesii* is here reported to have $2n=15_{II}$ (*Bierner 91-88*, see list of specimens examined).

Hymenoxys cooperi (as *H. biennis*) has been reported by Gao et al. (1990) to produce (among other compounds) sesquiterpene lactones very similar or identical to ones produced by other taxa in *Hymenoxys* subgenus *Picradenia* (e.g., Sanderson 1975; Seaman 1982). Recent unpublished work by Otmar Spring and Barbara Zitterell-Haid (personal communication) appears to confirm a high degree of similarity among the taxa of *Hymenoxys* subgenus *Picradenia* (including *H. jamesii*) with regard to sesquiterpene lactone content. Of note, their data suggest that *H. jamesii* may be chemically more similar to *H. subintegra,* a taxon restricted to the Kaibab Plateau of northern Arizona, than to *H. cooperi.*

Morphologic, cytologic, and chemical data are all consistent with the placement of *Hymenoxys jamesii* in *Hymenoxys* subgenus *Picradenia.* It is here recognized as a distinct species because it is completely allopatric to and morphologically distinct from the other taxa of *Hymenoxys.*

Hymenoxys jamesii Bierner, sp. nov.—Type: USA, Arizona, Navajo
   Co.: forest rd 504 (rd to Winslow from Heber), 5.9 mi NW of
   hwy 260 (jct just W of Heber), 12 Aug 1991, *Bierner 91-87*
   (holotype, TEX; isotypes, NY, US).

H. cooperi (A. Gray) Cockerell affinis sed capitulis parvioribus
numerosioribusque, ligulis parvioribus paucioribusque, et pappi
squamis brevioribus notabilis.

Plants apparently biennial, 6.0 ± 1.7 dm tall (range 3.5–11.4 dm;
n = 28) excluding the root. Stems usually 1, but sometimes 2–4 or
rarely as many as 15–20, paniculately to corymbosely branched
above, sulcate below becoming striate above, usually distinctly pur-
ple-red below becoming green above, usually moderately to densely
pubescent below becoming sparsely to moderately pubescent above,
but ranging from sparsely to densely pubescent throughout. Leaves
dotted with impressed glands, entire, simple to pinnately or bipin-
nately divided into 3–9 linear segments, terminal segment of mid-
stem leaves 1.4 ± 0.3 mm wide (range 0.8–2.2 mm; n = 61); basal
leaves in a dense rosette, usually divided into 5–7 segments, but
sometimes with as few as 3 or as many as 9 segments, usually sparsely
pubescent; lower leaves usually divided into 3–5 segments, but some-
times with 7 segments, sparsely to moderately pubescent; middle
leaves divided into 3–5 segments, sparsely to densely pubescent;
upper leaves simple or divided into 3(–5) segments, sparsely to densely
pubescent. Peduncles 2.6 ± 1.0 cm long (range 1.3–5.0 cm; n = 56),
striate, expanded apically, sparsely to densely pubescent below be-
coming moderately to densely pubescent above, sparsely to mod-
erately dotted with sessile glands below, becoming moderately to
densely dotted with sessile glands above. Heads 114 ± 65 per plant
(range 30–330; n = 28), subhemispheric to campanulate, 5.9 ± 0.7
mm high (range 4–7 mm; n = 59), 6.4 ± 1.0 mm in diameter (range
4–8 mm; n = 59) excluding the rays. Receptacle hemispheric to,
usually, conic, naked, 1.3 ± 0.3 mm high (range 1.0–2.0 mm; n =
20), 1.7 ± 0.4 mm in diameter (range 1.0–2.4 mm; n = 20). Invo-
lucral bracts in two morphologically distinct series; outer bracts
usually 8 or 9 per head (range 8–10; n = 18), united their lower one-
third, green and herbaceous, keeled, ovate to lanceolate, apex acute
to acuminate, outer surface sparsely to moderately pubescent, par-
ticularly along the margins, and sparsely to densely dotted with
sessile and(or) impressed glands, inner surface glabrous or some-
times sparsely pubescent at the apex, 3.5 ± 0.5 mm long (range 2.9–
5.5 mm; n = 86), 1.2 ± 0.3 mm wide (range 0.5–1.9 mm; n = 86);
inner bracts usually 10 ± 2 per head (range 8–14; n = 18), free,
usually slightly exceeding the outer bracts due to their higher point
of attachment, body yellow and scale-like, tip yellow-green to green
and herbaceous, weakly keeled, obovate, mucronate, outer surface

glabrous to moderately pubescent, particularly along the margins, and sparsely to moderately dotted with sessile glands, inner surface glabrous, 3.4 ± 0.4 mm long (range 2.8–4.2 mm; n = 111), 1.6 ± 0.3 mm wide (range 1.0–2.5 mm; n = 111). Ray florets carpellate, fertile, usually 8 per head (range 7–9; n = 18); ligules yellow, 3-lobed, tube glabrous to sparsely pubescent, upper surface glabrous and eglandular, lower surface sparsely pubescent and sparsely to moderately dotted with sessile glands, 6.5 ± 0.9 mm long (range 4.2–8.0 mm; n = 142), 3.3 ± 0.6 mm wide (range 2.3–5.0 mm; n = 141). Disc florets hermaphroditic, fertile; corollas yellow with yellow lobes, 5-lobed, the lower one-fourth to one-third usually constricted into a narrower yellow-brown tube, cylindric to cylindric campan-ulate, glabrous to densely pubescent and sparsely to moderately dotted with sessile glands, 2.6 ± 0.2 mm long (range 2.4–3.0 mm; n = 90), 0.5 ± 0.1 mm in diameter (range 0.4–0.8 mm; n = 90), the tube 0.7 ± 0.1 mm long (range 0.6–0.9 mm; n = 90). Achenes narrowly obconic, densely pubescent with straight, forked, antrorse hairs, 1.9 ± 0.1 mm long (range 1.6–2.1 mm; n = 90), 0.5 ± 0.1 mm in diameter (range 0.4–0.7 mm; n = 90). Pappus scales usually 5 (range 4–8; n = 115), obovate, apex rounded to obtuse to, usually, acuminate into an acute point or short awn, 1.3 ± 0.3 mm long (range 0.8–2.1 mm; n = 115) including the awn if present, 0.8 ± 0.1 mm wide (range 0.5–1.0 mm; n = 115), the awn when present 0.2 ± 0.1 mm long (range 0.1–0.4 mm; n = 26). Chromosome number: $2n=15_{II}$.

Distributed on the Mogollon Plateau of eastern central Arizona (Fig. 1). Flowering mainly in July and August.

Specimens examined. USA, ARIZONA, Coconino Co.: Blueridge Ranger Station, Coconino Forest, 7 Aug 1929, *Eggleston 23381* (LL); Sitgraves National Forest, Mogollon Rim, off hwy 160, 18 Aug 1970, *Correll & Correll 39422* (LL); hwy 87, 10.9 mi SW of turnoff to Happy Jack and Flagstaff, 9 Aug 1975, *Bierner 51384* (TEX); hwy 87, 7.7 mi SW of turnoff to Happy Jack, 30 Jul 1988, *Bierner 88-72* (TEX); forest rd 504 (rd to Heber), 2.9 mi S of hwy 99, 11 Aug 1991, *Bierner 91-84* (TEX). Gila Co.: 3 mi S of Pine along hwy 87, 19 Jul 1973, *Higgins 7849* (NY); hwy 87, 13.0 mi NW of hwy 260, just S of Pine, 9 Aug 1975, *Bierner 51382* (TEX); hwy 87, 14.1 mi NW of hwy 260, just S of Pine, 9 Aug 1975, *Bierner 51383* (TEX). Navajo Co.: Chevelon Crossing Campground, ca. 16 mi NW of hwy 260 on forest rd 504 (jct just W of Heber), 11 Aug 1991, *Bierner 91-85* (TEX); forest rd 504 (rd to Winslow from Heber), 11.5 mi NW of hwy 260 (jct just W of Heber), 12 Aug 1991, *Bierner 91-86* (TEX); forest rd 504 (rd to Winslow from Heber), 1.4 mi NW of hwy 260 (jct just W of Heber), chromosome number $2n=15_{II}$, 12 Aug 1991, *Bierner 91-88* (TEX).
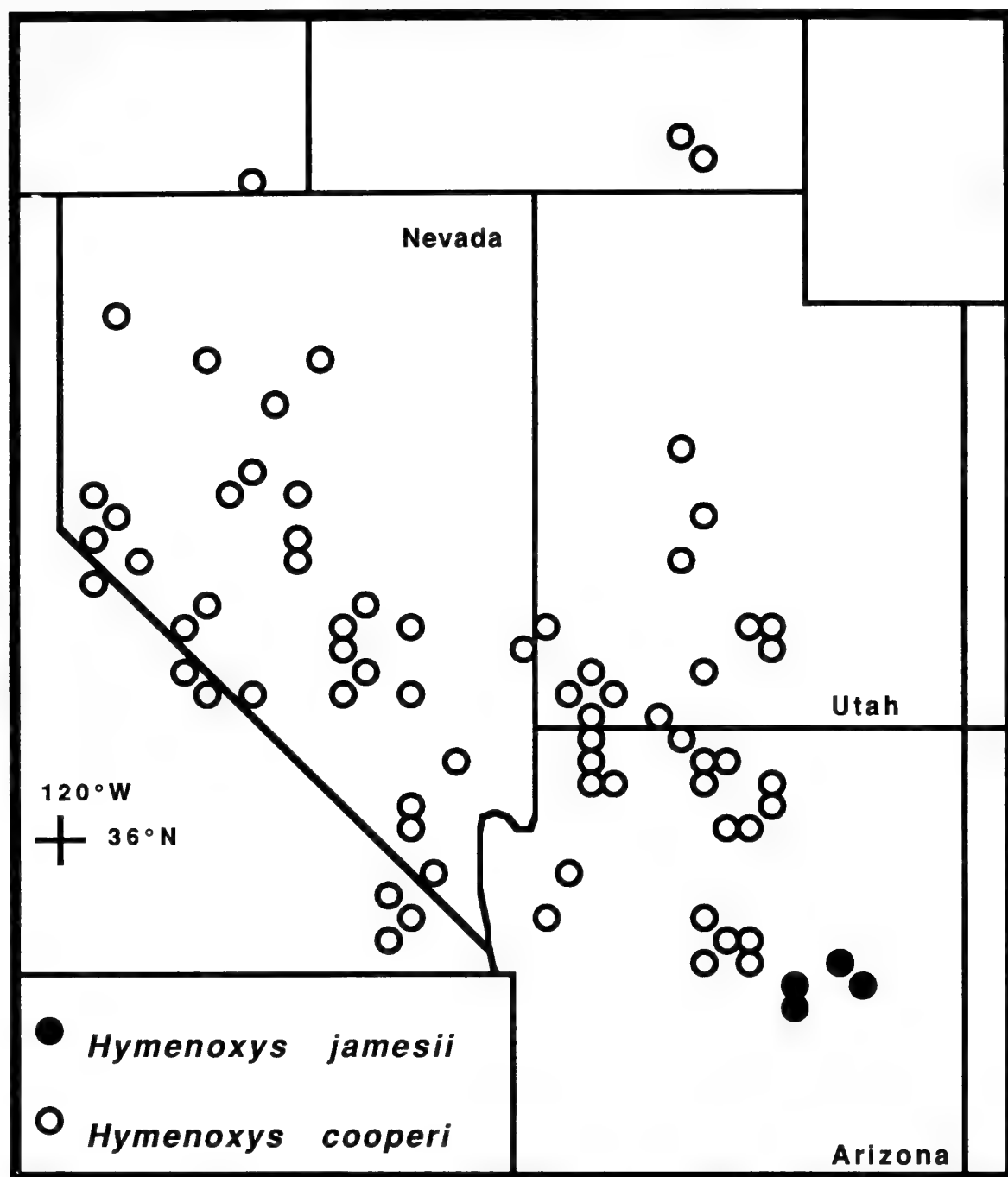
FIG. 1.   Distribution of *Hymenoxys jamesii* and *H. cooperi.*

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SEED GERMINATION IN THE EXOTIC SHRUB
CYTISUS SCOPARIUS (SCOTCH BROOM)
IN CALIFORNIA

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ABSTRACT

The germination characteristics of *Cytisus scoparius,* a weedy leguminous shrub now naturalized in California, were examined in the field and laboratory. Seed viability, longevity, and the effects of light, temperature, eliaosome removal and seed depth on germination were determined. Effects on seedling vigor of scarification by alternate immersion in liquid nitrogen and boiling water were appraised on fresh and stored *C. scoparius* seeds. Both fresh and stored seeds of a Sierra Nevada foothill population were found to be 98% viable, but >65% of *C. scoparius* seeds had an impervious seed coat that delayed germination for months or years. Permeable seeds emerge most successfully from the top 2 cm of soil, and none emerged from below 8 cm. Germination occurred at 4–33°C, maximally at 18–22°C. Heat of >150°C or more for 2 min killed the seed, and temperatures >100°C for 1 min increased susceptibility to fungal pathogens. Temperatures of 65°C for 2 min significantly increased germination and did not decrease fungal resistance. Eliaosome removal had no significant effect on seed germination. Alternate immersion in liquid nitrogen and boiling water did not effect seedling vigor and was effective in scarifying fresh and stored *C. scoparius* seeds.

Cytisus scoparius (L.) Link [*Sarothamnus scoparius* (L.) Wimmer ex Koch; Scotch broom; Fabaceae] is an alien invasive shrub species introduced into California from Europe in the 1850's as an ornamental (Geickey 1957). It is now naturalized in California, currently occupying >250,000 ha both in northwest coastal and Sierra Nevada foothill regions (L. Barbe personal communication). With a lifespan of up to 17 yr in California (Rejmánek unpublished data), *C. scoparius* produces a large quantity of seeds that continue to germinate at least 5 yr after seed sources are removed (Bossard and Rejmánek unpublished data). In the Sierra Nevada foothills, seed germination is initiated in mid-to-late November by the first biologically effective rains after the summer drought and continues through the first week in May. This species is diplochorous, containing an eliaosome on the seeds that attracts ants which gather the seeds and eat the eliaosome after their initial ballistic dispersal from the parent plant in July (Wiese 1909; Bossard 1990a). It is not known if this removal of the eliaosome by ants enhances germination of *C. scoparius* seed.

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C. scoparius is considered a noxious weed by botanists, conservationists and foresters in California since it aggressively displaces native plant species and makes reforestation difficult in some areas of the Sierra Nevada foothills (Andres 1979). It is equally problematic in Oregon and Canada (Miller personal communication), Australia (Waterhouse 1988) and New Zealand (Partridge 1989) where control programs have recently been instituted. Attempts to control the spread of *C. scoparius* and to remove it from areas it already occupies have met with a multitude of problems (Parsons 1973; Williams 1981; Bossard 1991; Smith and Harlen 1991). In light of the importance of germination characteristics to establishment, understanding *C. scoparius* germination traits and the range of heterogeneity of these traits is a necessary first step in creating a comprehensive management plan to control it.

This species can have an impervious seedcoat and be difficult to germinate once dried, unless it is scarified (Schopmeyer 1974; Browse 1979; Young and Young 1986). Preliminary investigations suggest alternate immersion in liquid nitrogen and boiling water is an effective means of scarifying *C. scoparius* seeds to enhance their simultaneous germination (Abdullah et al. 1989). This would facilitate obtaining even-aged cohorts of seedlings for use in basic or applied studies on this species. However, scarification treatments may effect the vigor of resultant seedlings. Further, such treatments may not effect fresh and stored seeds in the same way (Mayer and Poljakoff-Mayber 1982).

Here I discuss studies pertaining to *C. scoparius* seeds and their germination which had the following goals: to ascertain seed viability and longevity in the field; determine the effects of light, temperature, seed depth, and eliaosome removal on germination; and to further examine the effects of alternate immersion in liquid nitrogen and boiling water as a means of scarifying *C. scoparius* seeds.

Methods

Study Site

The field research site was a 2 ha area of the Eldorado National Forest (ENF), Eldorado County, California, dominated by *C. scoparius* interspersed with *Pinus ponderosa* Dougl. and (in spring) patches of annual grasses and forbs. The pines were planted 20 yr ago for reforestation. The area is 4 km east of the Georgetown Ranger Station in the northern yellow (Ponderosa) pine forest as described by Küchler (1988) at an elevation of 1067 m, with slopes of 1 to 9%. Soil is Maymen rocky loam 10–65 cm deep. Annual precipitation averages 142 cm with a range of 69–290 cm per year; almost no rain occurs from May to November. Total precipitation in 1987, 1988, and 1989 was 117 cm, 74 cm, and 110 cm, respectively (El-

dorado National Forest District Headquarters, Eldorado County, California).

Experimental Methods

All seeds used in these experiments came from bulk samples collected by hand at ENF. Seeds were collected from mature pods of *C. scoparius* shrubs one week after ballistic dispersal ensued. Seeds were collected 29 June, 1987 and stored at 4°C in opaque glass jars (stored seed) or collected 8 July, 1988 and used the next day (fresh seed).

1. Speed viability and moisture content. Viability of seeds stored 6, 9, and 12 months and fresh seeds from ENF was assessed via tetrazolium red tests (Mackey 1972; Moore 1972). Seeds were knicked, soaked 3 hr at 22°C, immersed in tetrazolium red for 8 hours at 22°C, then bisected with a razor blade and examined for staining. Moisture content of three groups of 200 seeds was tested via the low temperature method (Thomson 1979).

2. Seed longevity in the soil. To estimate the amount of seed germinating from a given year's seed crop over time, 1000 *C. scoparius* seeds collected June, 1987 were placed in each of eight 1 × 12 × 12 cm mesh bags. Four of the bags were placed on the soil surface and four others were placed 4 cm under the soil surface at the ENF research site in July, 1987. The seed bags were covered with a 60 × 60 × 30 cm exclosure made of 1.5 cm mesh chicken wire. In January, March, and May, 1988, 1989, 1990, the germination status of the seeds was recorded and the germinated seeds were removed from the bags.

3. Response to depth of planting. To ascertain the effect of planting depth on seedling emergence *C. scoparius* seeds stored 6 months were planted in 15 × 15 × 15 cm plastic pots filled with University of California, Davis, sandy loam greenhouse mix soil at depths of 0, 1, 2, 4, 6, 8 and 10 cm, then placed in a greenhouse with a temperature range of 20–25°C. Of the 20 seeds per treatment those seeds emerging were counted weekly for 8 weeks. There were three replicates of 20 seeds at each depth. At ENF in November, 1987, a 12 cm deep vertical walled trench was dug and 15 seeds were inserted 2 cm into the side of the trench in two places at each of the same depths used in the greenhouse study, then the trench was filled.

4. Response to temperature. The following methods apply to the response to temperature experiment and also to experiment 5 described below. For each pre-germination treatment, 25 stored seeds were plated in a 10 cm Petri dish lined with 2 circles of Whatman No. 1 filter paper kept moist with distilled water. Petri dishes were

placed in a growth chamber with the following settings: 15 L/9 D hr photoperiod (120 μmol m^{-2} sec^{-1}) and 23/16°C thermoperiod conditions comparable to those found in the field during the latter portion of the *C. scoparius* germination season (Bossard 1990b). The number of seeds imbibed (scored as a >50% increase in seed diameter) and the number of seeds germinated (scored as radicle protrusion of >2 mm) was recorded every 2 days the first week and every 3–4 days thereafter. In cases where fungal infection of the seeds occurred, the level of infection and fate of the seeds were recorded.

Temperature effects on germination were determined using a temperature step gradient bar (Grime et al. 1981) with temperatures set at 5, 10, 14, 18, 22, 26, 30, and 33°C. Seeds stored 7 months were used in this experiment. Each of two pre-germination treatments was replicated in four Petri dishes. Treatments were: 1. controls given no pre–germination treatment; 2. seeds alternatively immersed in boiling water and liquid nitrogen. In this treatment seeds were placed in cheese cloth bags and dipped for 3 seconds in boiling water then 15 seconds in liquid nitrogen. This alternation was done twice followed by just one second in boiling water to thaw the bag (hereafter hot/cold).

5. Response of fresh and stored seeds in Petri dishes to various pre-germination treatments. The effects on germination of exposure to light, removal of eliaosome, heat, and hot/cold scarifying of seeds were examined in two studies done June–August, 1988. Both seeds stored 11 months and fresh seeds were utilized for this experiment. The treatments were:

(1) controls (no pre-germination treatment, eliaosomes on),
(2) dark (each Petri dish was completely wrapped in aluminum foil and opened briefly for counting of germinants under a low intensity of green light),
(3) light (each Petri dish left exposed to growth chamber lights),
(4) eliaosome off (entire eliaosome removed with a tweezers from stored seed germinated in light),
(6) 65°C-60s, 65°C-120s (stored seeds placed in 65°C oven for 60 and 120 sec and germinated in light),
(7) 100°C-60s, 100°C-120s (stored seeds placed in a 100°C oven for 60 and 120 sec and germinated in light),
(8) 150°C-60s, 150°C-120s (stored seeds placed in 150°C oven for 60 and 120 sec and germinated in light),
(9) 200°C-60s, 200°C-120s (stored seeds placed in 200°C oven for 60 and 120 sec and germinated in light),
(10) hot/cold (as described above).

The oven was modified with sheet metal and aluminum foil so seeds could be introduced through a 2 cm by 12 cm opening while

allowing minimal heat escape. Duration of heat treatments was in-
tended to simulate the duration of change in temperatures in a flash
fire (Floyd 1966) typical of prescribed burns, since prescribed burn-
ing is one method expected to be used to remove invasive popu-
lations of *C. scoparius*. Maximum temperatures when measured at
2 cm below the soil surface during a prescribed burn at Eldorado
National Forest ranged from 59°C to 152°C depending on the fuel
load (Bossard unpublished). Temperatures chosen for this study ap-
proximated this range and were reported in other studies to stimulate
germination of legumes in the field (Quinlivan 1961, 1966; Floyd
1966; Martin et al. 1975; Shea et al. 1979; Auld 1986). Treatments
were replicated in four Petri dishes. Seeds not germinating were
tested for viability via tetrazolium red tests (Mackey 1972; Moore
1972).

6. *Response of seeds in soil to heating, alternating temperature
scarification*. To assess the vigor of the seedlings, the following ex-
periment was done using seed stored 9 months. Twenty-five seeds
each were placed in 15 × 15 × 15 cm plastic pots filled with Uni-
versity of California, Davis, sandy loam greenhouse mix soil, then
covered with 1.5 cm soil. Four previously described pre-germination
treatments were used:

(1) control (no pre-germination treatment),
(2) bake 65°C (placed in 65°C oven for 60 seconds),
(3) bake 100°C (placed in 100°C oven for 60 seconds),
(4) hot/cold

All pots were placed in the growth chamber with conditions as
described previously. There were four replications of each treatment.
The number of emerged seedlings was recorded for each pot every
two days during the first week and every 3–4 days thereafter.

Statistical analysis. Analysis was done using multiple regression
and ANOVA in Statview 512+. Data on the number of seeds ger-
minating were analyzed after angular transformation. Multiple mean
comparisons were conducted using Scheffé's test (Zar 1984).

RESULTS

Seed viability and moisture content. Ninety-eight percent of the 6,
9 and 11 month stored and freshly collected seeds were found to be
viable by the tetrazolium red test. Seeds stored 6 months had a
moisture content of 10.2%, while fresh seed had a moisture content
of 14.1%.

Seed longevity in the soil. There was no significant difference in
the proportion of seeds germinating at or 4 cm below the soil surface
(Table 1). About ⅔ of the seeds from the 1987 seed crop germinated

TABLE 1. FIELD GERMINATION OF *CYTISUS SCOPARIUS* SEEDS. n = 4 for each treatment.

Elapsed time from placement	On surface		4 cm below soil surface	
	Seeds germinated	Seeds remaining ungerminated	Seeds germinated	Seeds remaining ungerminated
6–11 months	65 ± 12%	35 ± 12%	64 ± 9%	36 ± 9%
18–23 months	20 ± 4%	15 ± 4%	24 ± 4%	11 ± 4%
30–35 months	10 ± 3%	5 ± 2%	4 ± 2%	7 ± 3%

in the field during the first year. By the end of the second germination season, <15% of the seed remained ungerminated.

Response to depth of planting. The largest proportion of seeds emerged from depths of 1 and 2 cm. In the greenhouse, there was little emergence of seed planted 8 cm or below and only 50% emergence from plantings at 6 cm (Fig. 1). At ENF, no seeds emerged below 6 cm.

Response to temperature. Some germination occurred at all temperatures for hot/cold and control seeds within 4 wk (Figs. 2 and 3). The hot/cold treatment increased rate and final germination percentage when compared to the controls. Hot/cold treatment seeds showed maximum germination at 18–22°C, whereas maximum germination for control seed occurred at 22–26°C.
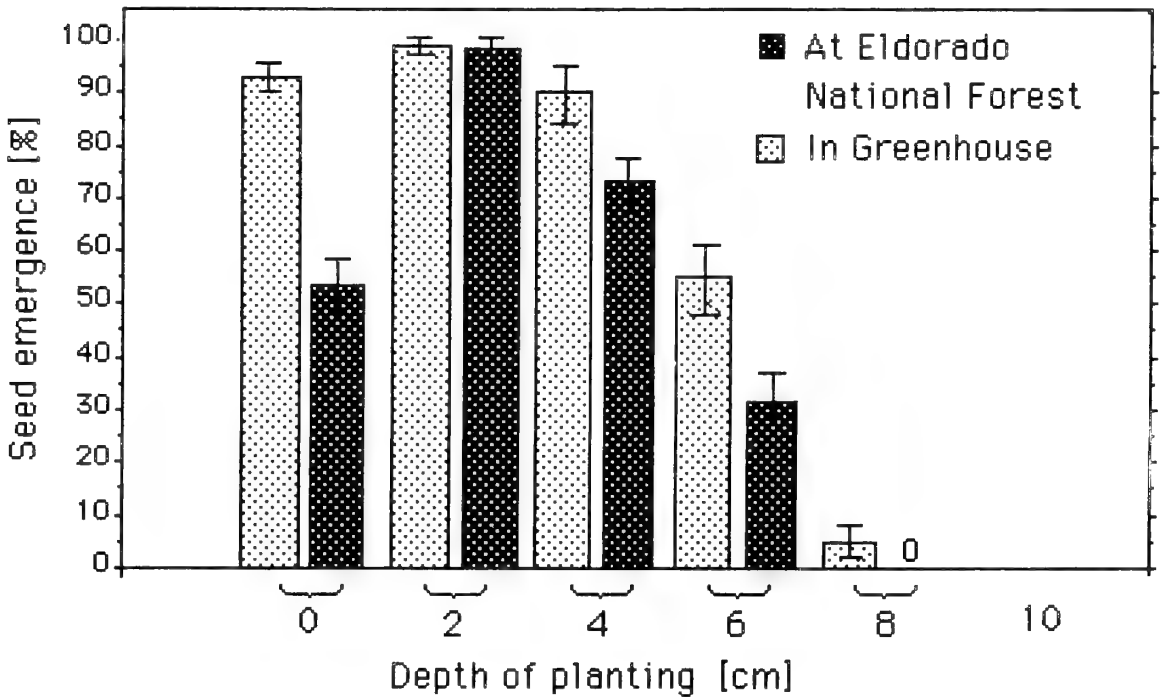
FIG. 1. The proportion of *Cytisus scoparius* seeds emerged from various planting depths in sandy loam in the green house and at Eldorado National Forest in naturally occurring rocky loam. Bars show 95% confidence intervals.

Key

○ 5C Control   □ 10C Control   ◆ 14C Control   ✕ 18C Control

5C Hot/cold   △ 10C Hot/cold   + 14C Hot/cold   ⊖ 18C Hot/cold

— — — — — — Controls

——————— Hot/cold treatment to make seeds permeable
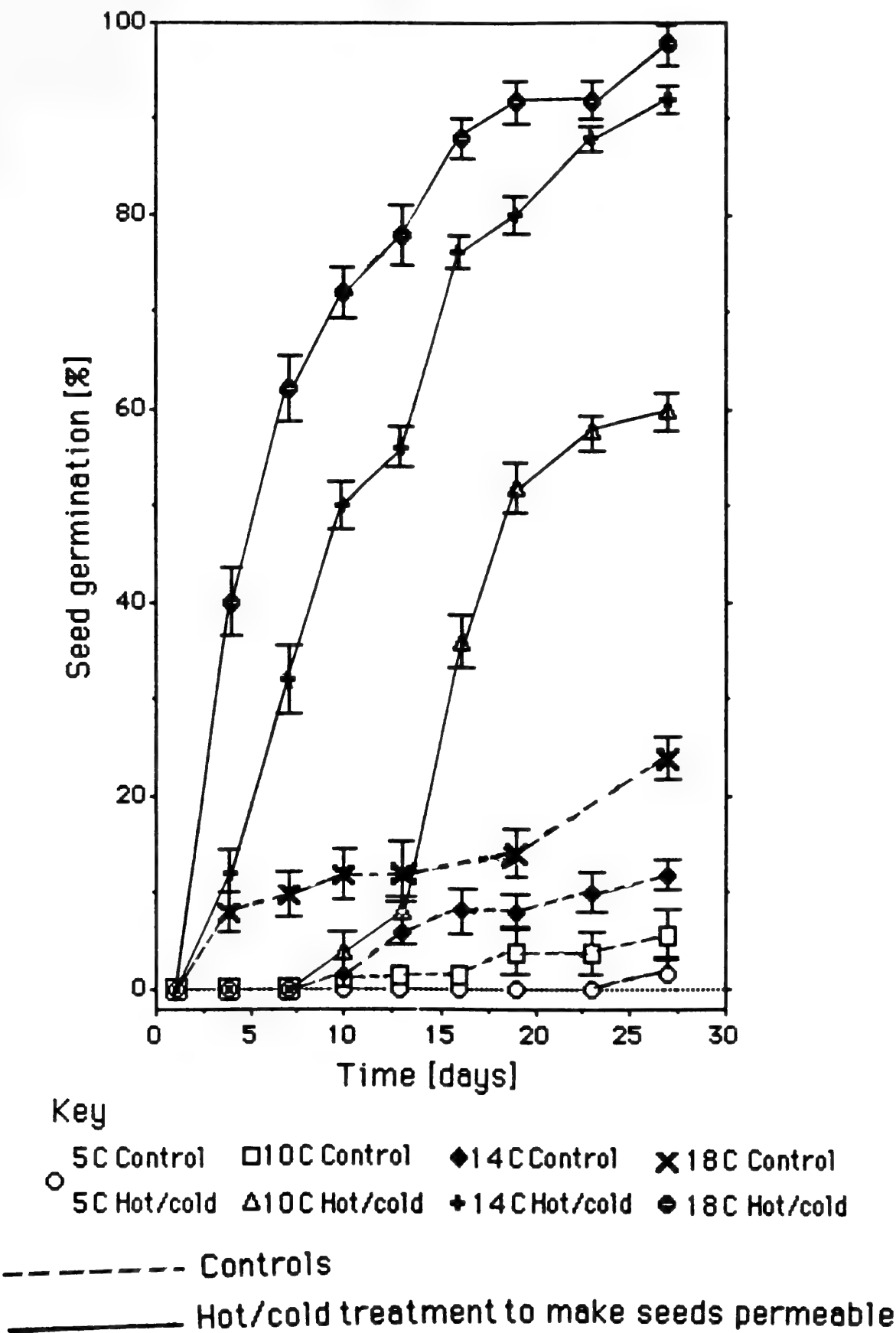
Fig. 2.   The proportion of *Cytisus scoparius* seeds germinating over 28 days at various constant temperatures between 5 and 18°C. Bars show 95% confidence intervals.
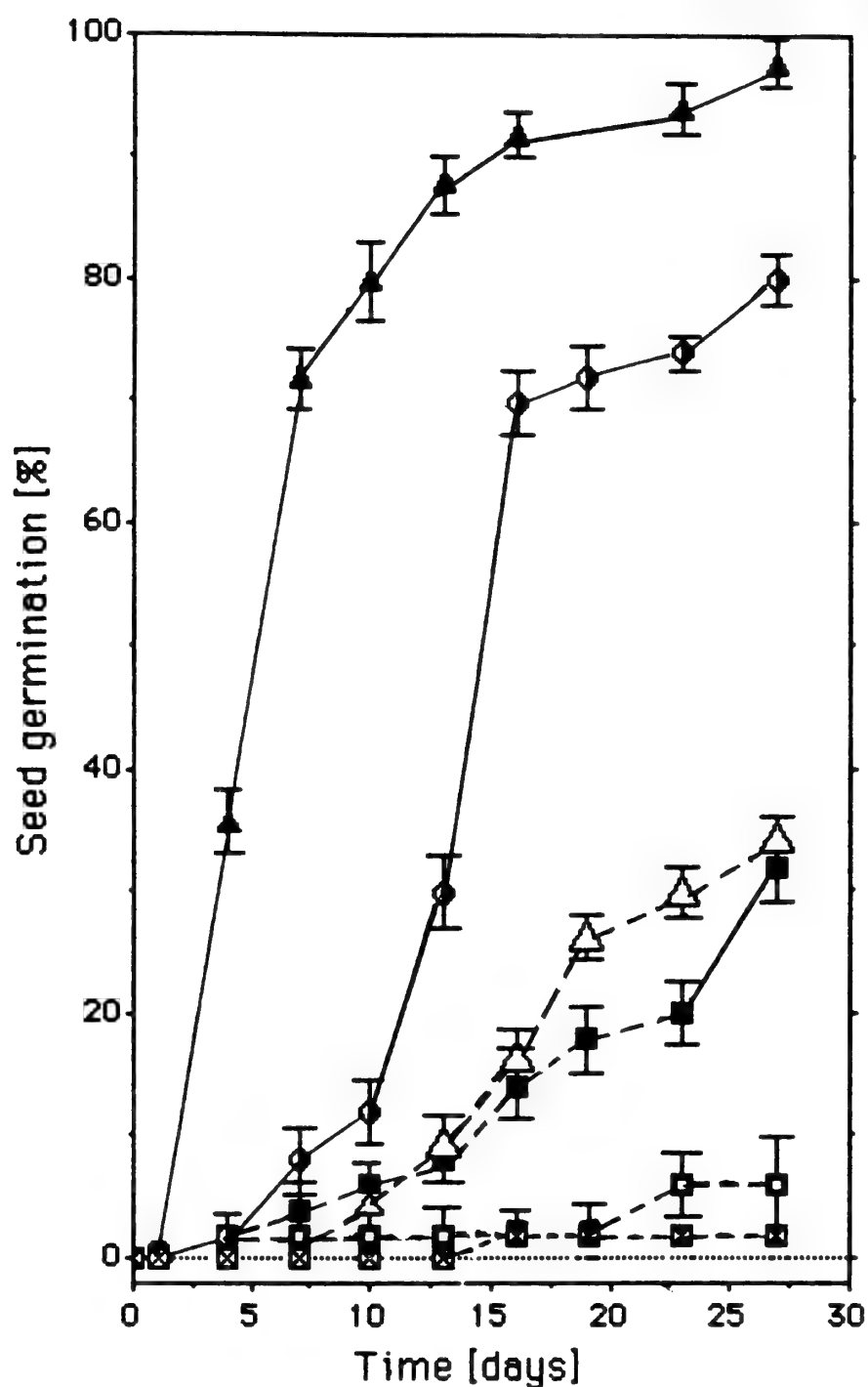
Key

■ 22 C Control   △ 26 C Control   30 C Control   33 C Control

▲ 22 C Hot/cold   ◉ 26 Hot/cold   30 C Hot/cold   33 C Hot/cold

— — — — — — Controls

———————— Hot/cold treatment to make seeds permeable

Fig. 3.   The proportion of *Cytisus scoparius* seeds germinating over 28 days at various constant temperatures between 22 and 33°C. Bars show 95% confidence intervals.
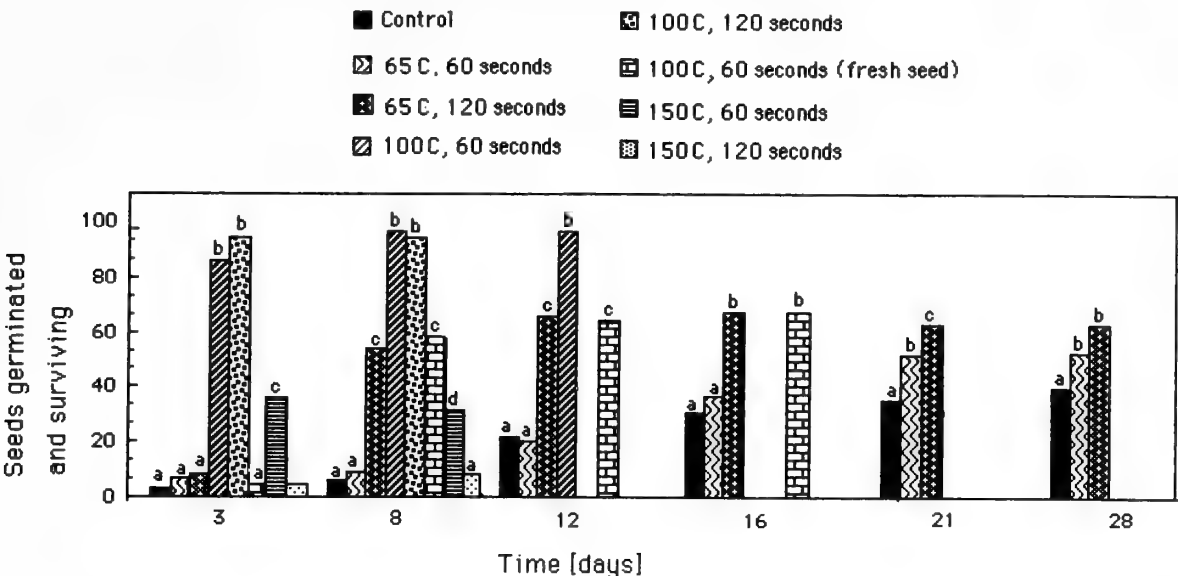
FIG. 4. The proportion of *Cytisus scoparius* seeds germinating and surviving after various heat treatments. For each date means with the same letters are not significantly different at the 0.05 level.

Response of fresh and stored seed in Petri dishes to various pre-germination treatments. An ANOVA repeated measure analyses of independent variables, eliaosome removal and date on the dependent variable, number of seeds germinated in 32 days, showed eliaosome removal had no significant effect (F = 0.92; P > 0.05).

The effect of light on seed germination varied somewhat with the age of the seeds but the differences were not statistically significant (Table 2). At least 34% of control seeds germinated regardless of light conditions. The hot/cold treatment elicited significantly more germination on stored seed than on fresh seed. It resulted in the highest proportion of seeds germinating and did not diminish the vigor of the seedlings. Heating the seeds stimulated significantly more germination in stored than fresh seeds, but in all heat treatments (except 65°C) seedlings died of fungal infections by the 15th day of incubation (Fig. 4). Seeds baked 60 and 120 sec at 200°C did not germinate. Tetrazolium red tests revealed 100% of ungerminated control and 65°C heated seed was viable. One hundred percent of ungerminated 150°C seed heated 120 seconds and all ungerminated 100°C and 200°C heated seed was not viable. Ninety-two percent of ungerminated 150°C seed heated 60 seconds (62 of 64 seeds) was not viable.

Response of seeds in soil to heating and alternating temperature scarification. — For seeds planted in soil, the hot/cold pre-treatment was the most successful in increasing emergence (Fig. 5). Examination of the pots containing 100°C heat treated seeds after seven days revealed that 96% of the seeds had germinated, but died of fungal infections before emerging.

TABLE 2. THE PROPORTION OF *CYTISUS SCOPARIUS* SEEDS GERMINATING AND SURVIVING AFTER VARIOUS PRE-GERMINATION TREATMENTS. An ANOVA revealed treatment means with + are significantly different at the 0.05 level, with ++ significantly different at the 0.01 level using Scheffé's tset. # Seedlings died from fungal infections in these two treatments.

Treatment	Seeds germinated [mean %] 12 days after plating	Range	Treatments 1	2	3	4	5	6	7	8	9	10
(1) Control, stored, light	14	12–16										
(2) Control, stored, dark	17	16–20										
(3) Control, fresh, light	30	24–36										
(4) Control, fresh, dark	19	16–24										
(5) Bake 100°C, stored	97	96–100	++	++	++	++						
(6) Bake 100°C, fresh	69	68–72	++	++	++	++	+					
(7) Hot/cold, stored, dark	82	80–88	++	++	++	++						
(8) Hot/cold, fresh, dark	75	72–80	++	++	++	++	+					
(9) Hot/cold, stored, light	84	80–88	++	++	++	++						
(10) Hot/cold, fresh, light	68	68–68	++	++	++	++	+					

Treatment	Seeds germinated and surviving 32 days after plating [mean %]	Range	Treatment 1	2	3	4	5	6	7	8	9	10
(1) Control, stored, light	34	32–36										
(2) Control, stored, dark	39	36–40										
(3) Control, fresh, light	50	48–52										
(4) Control, fresh, dark	39	36–44										
(5) Bake 100°C, stored	6#	4–8										
(6) Bake 100°C, fresh	6#	4–8										
(7) Hot/cold, stored, dark	95	92–96	++	++	++	++	++	++	+			
(8) Hot/cold, fresh, dark	82	80–84	++	++	++	++	++	++		+		
(9) Hot/cold, stored, light	98	96–100	++	++	++	++	++	++				
(10) Hot/cold, fresh, light	89	88–92	++	++	++	++	++	++			+	
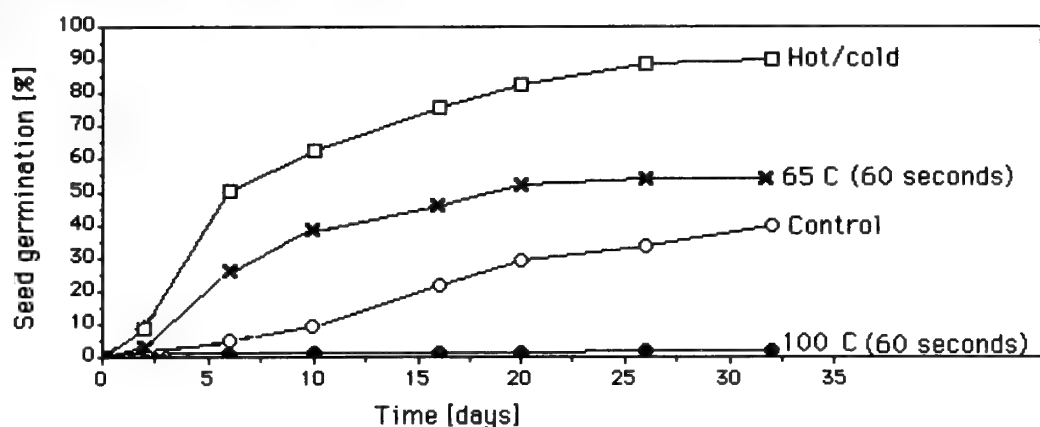
FIG. 5. The proportion of *Cytisus scoparius* seeds emerged from the soil after receiving various pre-germination treatments.

DISCUSSION

Almost 100% viability, in both fresh seed and seed stored up to 2 yr, was found in this study. Although possessing high viability 60% of *C. scoparius* seeds from ENF contain impervious seed coats which prevent germination in field or laboratory until these seeds become permeable. This species' seeds have a range of phenotypic expression of both within- and between-year germination. While 40% of the seeds can germinate immediately upon dispersal and another 25% germinated sometime during the first year after deposition, at least 7% remain ungerminated after three years in the soil allowing the development of a large seed bank. Variability in the duration between seed deposition and germination provides *C. scoparius* with considerable flexibility for coping with the intra- and inter-yearly fluctuations in precipitation and temperature typical of California's Mediterranean climate.

In the laboratory, no more than 50% of unscarified seed of the ENF population germinated in any of the experiments within 32 days. This contrasts sharply with the findings of Grime et al. (1981) on germination of an English population of *C. scoparius* in which 73% of freshly collected seed and 90% of the seed stored 6 months at 5°C in jars germinated in 15 days.

Differences in the germination characteristics between seeds of these two populations could be caused by preconditioning, i.e., differences existing in the environments under which the seeds matured (Baskin and Baskin 1973), post-dispersal conditions, or genetic differences. Aitken (1939) found the degree and duration of hardseededness in several Fabaceous species depended on the amount of time existing for deposition of suberized materials in the seed coat (Aitken 1939; Brown 1955) and the degree of dehydration attained by that seed (Aitken 1939; Hyde 1954; Quinlivan 1968; Williams and Elliot 1966). The degree of desiccation experienced by the seeds of the California population, where relative humidity in the summer de-

clines to 10%, is considerably more than that experienced by the English population exposed to a minimum relative humidity of 54%. Since the European progenitors of the ENF population arrived in the California foothills >120 yr ago, it is possible ecotypic differentiation has occurred. Researchers on other leguminous species have reported significant differences in hardseededness for different varieties of *Melilotus alba* (Stevenson 1937) and *Trifolium repens* (Burton 1940). However as Baskin and Baskin (1973) and Quinn (1977) assert, when environmental explanations for the variations in seed germination characteristics exist, no genetic basis for those differences should be assumed without further research. Consequently, at this time the exact basis for differences in seed germination responses between populations in California and England cannot be ascribed.

Germinating *C. scoparius* seeds emerged most successfully from the top 2 cm of soil, although a few seeds gave rise to emergent seedlings from a depth of 6 cm in the field and even 8 cm in the sandy loam soil used in green house trials. Seeds found in abandoned *Aphaenogaster occidentalis* nests below 6 cm depth (Bossard 1990b) are therefore likely to represent lost genets of *C. scoparius*. Auld (1986) observed a similar situation for *Acacia suaveolans* in Australia; maximum field germination depth was 6 cm in this species, but seeds in ant nests were often as deep as 10 cm.

Temperatures provide minimal barriers to germination of *C. scoparius* seeds. The broad range of temperatures at which seeds from the ENF population can germinate may partially explain the ability of this woody weed to establish in many geographic areas with a variety of climates, and they are consistent with the long germination period observed for *C. scoparius* in the field at ENF. Almost 100% germination was attained in constant temperature conditions after pre-germination treatments which made the seeds permeable. Apparently, it has no physiological requirement for a cold period or variable day/night temperature for germination such as that found by Hagon (1971) in *T. subterraneum*.

The hot/cold treatment successfully enhanced germination of *C. scoparius* in Petri dishes and in soil without decreasing the vigor of the resultant seedlings. The greater enhancement of germination of stored seed than fresh seed by this technique is likely due to the greater level of desiccation existing in the stored seed. This is a useful method for scarifying this seed.

The findings of this study add credence to Baskin and Baskin's (1989) proposition that temperature is the most important environmental factor in the breakdown of the leguminous strophioles that maintain seed impermeability under natural conditions. Germination was significantly lower ($P < 0.001$) in unscarified seeds stored at a constant 4°C for seven months and then kept at constant op-

timum temperature on the temperature gradient bar than for unscarified seed exposed to the fluctuating temperatures in the field for 9 months. Daily range in summer ground temperature at the research site was 30–55°C day and 15 to 25°C night (Bossard unpublished data), comparable to daily fluctuations of summer temperature found by Quinlivan (1961, 1968) to make small herbaceous legume seeds permeable in the field.

Heating seeds to temperatures between 65 and 100°C stimulated germination. While seeds heated to 100°C for 60 or 120 seconds had almost 100% germination, all seedlings from that treatment and those from the 150°C heat treatment died from fungal infections by the fifteenth day after treatment. Parker and Kersnar (1989) found that germination of *Cytisus monspessulanus* seeds also was enhanced by 100°C heat for 60 sec but that the resulting seedlings suffered an increased rate of mortality. Temperatures of 150°C even for 60 sec made the majority of *C. scoparius* seeds non-viable. Temperatures of 65°C for 2 min significantly increased germination compared to that of controls (62% versus 42%) and did not increase the seedling mortality rate from fungal infection.

These results indicate that prescribed burns of areas infested with these shrubs could greatly decrease the number of seeds on and in the soil if burns are done under conditions that maximize soil heating so as to flush germination of seeds prior to the summer drought period at ENF. Research on the feasibility of depleting *C. scoparius* seedbanks by prescribed burning is in process.

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NOTES

QUERCUS DOUGLASII (FAGACEAE) IN CALIFORNIA'S CENTRAL VALLEY.—John C. Hunter, Botany Department, University of California, Davis, CA 95616.

In Northern San Joaquin County, *Quercus douglasii* (blue oak) occurs near the center of the Valley at the Liberty Cemetery (R6E T5N S36 SW¼). A dominant of woodlands surrounding the Central Valley, *Quercus douglasii*'s previously recorded distribution on the Central Valley's floor is limited to areas adjacent to the foothills and to Arbuckle soils in the Dunnigan-Arbuckle area (Griffin and Critchfield, USDA Forest Service, Research Paper PSW-82, 1972).

There are 14 blue oaks in the Liberty Cemetery and a number scattered on adjacent lands. These trees range from 15 to 120 cm DBH with most between 50 and 100 cm DBH. The area's soil is San Joaquin Loam which is derived from alluvium and has a well developed profile with hardpans (Weil, Soils of San Joaquin County, Agricultural Experiment Station, University of California, Berkeley, 1952). San Joaquin soils are distributed from eastern San Joaquin County to west of Thornton near the delta.

This site contributes to evidence that the Central Valley's vegetation did not consist of simply riparian forest and prairie. Early observations of the Valley include references to wooded plains, scrub oak, and brush (Weil 1952; Dawdy, USDA Forest Service, General Technical Report PSW-110, 1989). Based on these observations, other records, and extant vegetation, it seems possible that the pre-settlement prairie included areas of woodland, savannah, and scattered shrubs, and that other "foothill" species besides *Quercus douglasii* may also have been present on the Central Valley floor.

INVASION OF *AMORPHA FRUTICOSA* L. (LEGUMINOSAE) ALONG THE COLUMBIA AND SNAKE RIVERS IN OREGON AND WASHINGTON.—Judith B. Glad, 1400 N Holman, Portland, OR 97217 and Richard R. Halse, 4535 NW Big Oak, #3, Corvallis, OR 97330.

Amorpha fruticosa L. (indigobush, false indigo, bastard indigo) is a shrub native from southern Quebec, Canada, south to Florida, west into northern Mexico, southern California, and Wyoming, and north to Manitoba, Canada (Wilbur, Rhodora 77: 377–409, 1975). Barneby (Intermountain Flora IIIB:28, 1989) writes that *A. fruticosa* is occasional in Utah gardens and has become a fully established riparian weed along the Boise and Payette rivers in southwestern Idaho; he states that the genus is absent from the Pacific Northwest. The plant is not mentioned in Davis' Flora of Idaho (1952) or in the Flora of the Pacific Northwest (1973).

Amorpha fruticosa is firmly established along the Snake River in Baker and Malheur counties, OR, and in Garfield, Franklin, and Walla Walla counties, WA. Along the Columbia River, it has been found from the Hanford Reach in Benton and Franklin counties, WA, to Multnomah County, OR, and to Wahkiakum County, WA. It has also been reported on Deadman Creek upstream from Central Ferry (Garfield County, WA), above Starbuck on the Tucannon River (Columbia County, WA), along Mill Creek near the town of Walla Walla (Walla Walla County, WA), and along the Umatilla River in Oregon.

Collections have been made in Umatilla, Sherman and Morrow counties, OR, and Garfield County, WA (IDF, OSC). The first published report of the species in the

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Pacific Northwest was west of Rooster Rock State Park and at Dalton Point, Mult-
nomah County, OR, and at Home Valley, Skamania County, WA, by Jolley (Wild-
flowers of the Columbia Gorge, 1988). He called it *A. occidentalis* Abrams. These
plants have been identified as *A. fruticosa* by the authors. Additional collections from
along the Snake and Columbia Rivers have been made by the authors between 1989
and 1991.

In its native geographic range, *A. fruticosa* occurs along streams, on rocky banks,
in open wet woods, on pond shores, in ravines, and along roadsides (R. L. McGregor,
Amorpha in Great Plains Association, Flora of the Great Plains, 1986). In Oregon
and Washington the species occurs in the upper fluctuation zone of run-of-the-river
reservoirs along the Columbia and Snake Rivers and the upper drawdown zone of
storage reservoirs elsewhere. It also occurs along the banks of some smaller streams.
The usual substrates are rock, including riprap, and sand. The species is found along
an elevational gradient from 647 meters MSL in Malheur County, OR, to 6 meters
in Wahkiakum County, WA. Its common associates west of the Cascade Range are
Rubus spp., *Salix* spp., *Phalaris arundinacea* L., and *Alnus* sp. East of the Cascade
Range, it is commonly associated with *Artemisia* spp., *Centaurea* spp., *Lepidium
latifolia* L., *Phalaris arundinacea, Salix* spp., *Dipsacus sylvestris* L., *Rumex* spp.,
Bromus tectorum L. and *Sisymbrium* sp.

The source of this invasion by *A. fruticosa* cannot be determined with accuracy.
The most likely seed source is along the Boise River in Idaho, where the species may
have been planted by the CCC in the 1930's. It is possible that the species may have
been introduced more than once.

Amorpha fruticosa occurs in dense thickets along the Snake and Columbia rivers
from the Boise Valley to Hood River County, OR. From Hood River westward, its
abundance seems to decrease, so that thickets are uncommon but individual shrubs
are frequently seen. This distribution indicates an upstream seed source. The relative
scarcity of the species west of the Cascade Range may indicate that it is not well
adapted to the area. Individual plants seem as robust as those to the eastward,
however, so the more likely explanation is that the initial introduction occurred to
the east and the plants are spreading to the west slowly. In time perhaps the rivers'
edge will support a dense thicket of shrubs all the way to the Pacific Ocean.

EVIDENCE OF MULTIPLE INTRODUCTION OF *CRUPINA VULGARIS* IN INFESTATIONS IN THE
WESTERN UNITED STATES.—Michèle Couderc-LeVaillant, Laboratoire de Biologie,
Végétale, Muséum National d'Histoire Naturelle, 61, rue de Buffon 75005, Paris,
France and Cindy Talbott Roché, Department of Natural Resource Sciences, Wash-
ington State University, Pullman, WA 99164-6410.

An invasion pattern characterized by disconnected, widely separated populations
of *Crupina vulgaris* Pers. (Asteraceae: Cynareae) in the western United States em-
phasizes the importance of investigating the origin of infestations. Following its de-
tection in Idaho in 1968 (Stickney, Madroño 21:402, 1972), *Crupina vulgaris* was
found in Santa Rosa, California, in 1975 (Davis and Sherman, Madroño 38:296,
1991); Chelan County, Washington, in 1984 (Environmental assessment for exotic
vegetation management in the Upper Lake Chelan Basin, USDA Forest Service,
1991); Umatilla County, Oregon, in 1987; again in Sonoma County, California, in
1989 and in Modoc County, California, in 1991 (D. Barbe, California Department
of Food and Agriculture, personal communication). To date all reports have been of
a single taxon, which concurs with the hypothesis of a single introduction. However,
Patterson and Mortensen (Weed Science 33:333–339, 1985) doubted that the Cali-

fornia infestation could have come from the first detected introduction in Idaho and suggested a detailed taxonomic study of the introduced *Crupina* populations to determine their origin.

This suggestion is valid, but the studies must be based on knowledge of *Crupina* in the Eastern Hemisphere where it is native. Fortunately, extensive taxonomic, cytogenetic and biological studies have been conducted on the three taxa within the genus *Crupina* (Couderc, Origine hybride du *Crupina intermedia* Briq. et Cavill., Colloques internationaux du CNRS, La flore du bassin méditerranéen: essai de systématique no. 234, 531–536, 1974). This note reports the preliminary results of a collaboration which relates the *Crupina* populations introduced in North America with native populations in the Old World.

Achenes from four North American populations of *Crupina,* including Sonoma County, California; Harpster Grade, Idaho County, Idaho; Umatilla County, Oregon; and Chelan County, Washington, were examined to determine their taxonomic status. Among the five varieties of *Crupina vulgaris* cited in the literature, only two varieties are relevant to this study, the varieties *typica* Beauv. and *brachypappa* Beauv. These two varieties are easily and indisputably distinguished by the achenes (Couderc-LeVailllant, L'amphiploïdie dans le genre *Crupina* Dc., Essai de systématique synthétique, Thèse Docteur es Sciences, Univ. Paris-Sud, Orsay, 1984). Achenes of the two varieties differ in middle length of the achene and pappus. In *C. vulgaris* var. *typica,* the length of the achene varies from 4 to 5 mm and the length of the longest pappus silk ranges from 7 to 8 mm, depending on the origin (European populations). In *C. vulgaris* var. *brachypappa,* variation in the same characters is 3.5 to 5.0 mm and 4 to 5 mm, respectively (European populations). Although differences in pappus length provide a clearer differentiation, mean achene length also distinguishes between the two varieties, even if the range of values overlap. These size differences are not influenced by biotype or by environmental conditions as demonstrated by experimental culture.

Achenes from the Idaho population in 1991 varied in length from 3.75 to 5.0 mm; $n = 27$, the 95% confidence interval (C.I. 0.95) was 4.52 ± 0.13 mm. The length of the pappus silk varied from 7.0 to 9.0 mm (C.I. 0.95, 7.98 ± 0.19 mm). These values identify the Idaho population as *C. vulgaris* var. *typica.* Achenes from California and Oregon were within the same range, indicating that these populations are also variety *typica.*

Measurements of the same characteristics on achenes from the Washington population were significantly different. Achene length varied from 4.0 to 5.0 mm (C.I. 0.95, 4.16 ± 0.10 mm). The longest pappus silk varied from 4.50 to 6.0 mm (C.I. 0.95, 5.14 ± 0.11 mm). These measurements placed the Washington population in variety *brachypappa.*

By finding *Crupina vulgaris* var. *typica* in California, Idaho and Oregon and var. *brachypappa* in Washington, we have shown that *Crupina* invaded North America by multiple introduction, with at least two distinct origins.

In Europe the natural populations are generally isolated and homogeneous, but hybridization between the two varieties is possible. According to Briquet (Carpologie du genre *Crupina,* Candollea 4:241–278, 1930), var. *brachypappa* occurs only in the high valley of Durance in France. However, this does not indicate that Durance is the source of the Washington population because later work has established that variety *brachypappa* is much more widespread, occurring in other locations in France, as well as Switzerland, Spain, Greece and Romania (Couderc-LeVaillant 1984).

The fact that *Crupina* was introduced as multiple introductions underscores the importance of a comprehensive taxonomic study of North American populations in relation to Mediterranean sources of introduction. As a federal noxious weed, it is prohibited to import *Crupina* into the United States or to move it across state lines. However, not only the source, but the means of the introductions to this continent remain unknown. The addition of the remaining two species of *Crupina, C. crupinastrum* and *C. intermedia,* could substantially worsen the invasion problem. *Crupina*

intermedia is a stable amphiploid resulting from the crossing of *C. vulgaris* with *C. crupinastrum*. With its hybrid vigor, *C. intermedia* is larger and more competitive than either of its parents, with whom it does not hybridize. It has demonstrated its aggressiveness by replacing the parent species and expanding its range in parts of the Mediterranean region (H. Couderc, R. Gorenflot, M. Couderc, and J. Moret, Variation chromosomique d'Angiospermes et Collections Vivantes, Jardins botaniques et Arboretums de demain, Bureau des Ressources Génétiques, 155–165, 1991).

In addition to its practical value, the study of origins and characteristics of *Crupina* in North America by comparing it to native Mediterranean populations provides insight into the behavior of invading species.

NEW COMBINATIONS IN *RHAMNUS* (RHAMNACEAE).—John O. Sawyer, Jr., Department of Biological Sciences, Humboldt State University, Arcata, CA 95521.

Rhamnaceae in the forthcoming revision of Jepson's Manual of the Flowering Plants of California will have the following taxonomic changes based on study of specimens in the field and at CAS, HSC, JEPS, RSA, and UC.

In his 1938 monograph, (Monographs of the Rancho Santa Ana Botanical Garden, Botany Series 1) C. B. Wolf recognized six subspecies in *Rhamnus californica* Eschsch. Two have leaf blades ± glabrous on the lower side (*R. c.* ssp. *californica, R. c.* ssp. *occidentalis*) and four have leaf blades tomentose on the lower side (*R. c.* ssp. *crassifolia, R. c.* ssp. *cuspidata, R. c.* ssp. *tomentella, R. c.* spp. *ursina*). Because I consider *R. tomentella* Benth. as distinct from *R. californica* the following new combinations are necessary:

Rhamnus tomentella Benth. ssp. *crassifolia* (Jepson) J. O. Sawyer, comb. nov. Based on *R. californica* Eschsch. var. *crassifolia* Jepson, Man. Fl. Pl. Calif., p. 615. 1925. Ridge west of Bear Valley, western Colusa Co., *W. L. Jepson 8974.* Synonyms: *R. californica* Eschsch. ssp. *crassifolia* (Jepson) C. B. Wolf, Mon. Rancho Santa Ana Gard. Bot. Ser. 1:68. 1938.

Rhamnus tomentella Benth. ssp. *cuspidata* (E. Greene) J. O. Sawyer, comb. nov. Based on *R. cuspidata* E. Greene, Leafl. Bot. Obs. & Crit. 1:64. 1904. Near Tehachapi, Kern Co., Calif., n. d., E. I. Greene, June 22, 1889. Synonyms: *R. californica* Eschsch. var. *viridula* Jepson, Man. Fl. Pl. Calif., p. 615. 1925 [as *virida*]. Cottonwood Creek, 7500', *W. L. Jepson 5086, R. californica* Eschsch. ssp. *cuspidata* (Benth.) C. B. Wolf, Mon. Rancho Santa Ana Gard. Bot. Ser. 1:72. 1938.

Rhamnus tomentella Benth. ssp. *tomentella.* Pl. Hartw. 303. 1848. The Sierra Nevada foothills, collected by Hartweg. Synonyms: *R. californica* Eschsch. var. *tomentella* (Benth.) Brew. & Wats., Cal. Calif. 1:101. 1876. *R. californica* Eschsch. ssp. *tomentella* (Benth.) C. B. Wolf, Mon. Rancho Santa Ana Gard. Bot. Ser. 1:70. 1938.

Rhamnus tomentella Benth. ssp. *ursina* (E. Greene) J. O. Sawyer, comb. nov. Based on *R. ursina* E. Greene, Leafl. Bot. Obs. & Crit. 1:63. 1904. On Bear Mt. near Silver City, New Mexico, O. B. Metcalfe 172. Synonyms: *R. californica* Eschsch. ssp. *ursina* (E. Greene) C. B. Wolf, Mon. Rancho Santa Ana Gard Bot. Ser. 1:74. 1938.

NOTEWORTHY COLLECTIONS

CALIFORNIA

KOBRESIA BELLARDII (All.) Degland (CYPERACEAE).—Mono Co., Mono Basin, Cooney Lake, Virginia Creek drainage near the lake outflow, T2N, R24E, SE¼ sect. 1, 28 July 1988, *D.W. Taylor 9994* (UC, SJSU); *Glenn L. Clifton 18328* (PUA), 3102 m (10,180 ft) elevation, in small (ca. 4 m by 10 m) subirrigated strip on the lakeshore, in a dense sod dominated by *Carex subnigricans* Stacey.

Significance. Second known locality in California for this circumboreal sedge. The species is disjunct some 528 km (330 mi) from the Steens Mountains, Harney County, Oregon (K. Urban, unpublished checklist, Blue Mountain Community College, Pendleton, OR, 1981, cf. G. L. Bender, Reference Handbook on the Deserts of North America, Greenwood Press, Westport, CN, 1982), although Cronquist et al. (Intermountain Flora, Vol. 6, Columbia University Press, New York, NY, 1977) record it in Oregon only from the Wallowa Mountains (cf. G. Mason, Guide to the Plants of the Wallowa Mountains of Northeastern Oregon, Museum of Natural History, Univ. Oregon, Eugene, OR, 1975). The nearest occurrence to the east is ca. 880 km (500 mi) across the Great Basin in the Uinta Mountains, Utah (S. Goodrich and E. Neese, Uinta Basin Flora, USDA Forest Service, Ogden, UT, 1986). Major and Bamberg (Madroño 17:93–109, 1964) were the first to report *K. bellardii* from California, where it is commonly encountered on calcareous substrates (marble or calc-hornfels) at or above timberline in the Convict Creek basin (R. Pemble, Ph.D. dissertation, Univ. California, Davis, CA, 1970), some 64 km (40 miles) S in the Sierra Nevada. At Cooney Lake, *K. bellardii* is confined to a narrow band of marble (R. Kistler, U.S. Geological Survey Map GQ-462, 1966) forming the lakeshore, a setting ecologically analogous to occurrences in the Convict Creek Basin.

—DEAN W. TAYLOR and GLENN L. CLIFTON, BioSystems Analysis Inc., Santa Cruz, CA, 95006.

WASHINGTON

PLATANTHERA CHORISIANA (Cham.) Reich. (ORCHIDACEAE).—Snohomish Co. Mt. Baker-Snoqualmie National Forest, Henry M. Jackson Wilderness Area, subalpine meadows around pools NE of Silver Lake among *Dodecatheon jeffryi* van Houtte, T29N, R11E, S28, NW¼, SW¼, NE¼, elev. 4300 ft (1290 m), 20 Aug 1980, *A. E. Grable 8158* (WS, WTU); same location, *A. E. Grable 8633* (WS); 150 m east of previous location, drying marsh partially shaded by *Chaemycyparis* and *Tsuga,* 10 Aug 1986, *A. E. Grable 10920* (WS).

Previous knowledge. Northern Japan; coastal Russia, Alaska, and British Columbia; and Snohomish Co., Washington (C. A. Luer, The native orchids of the United States and Canada excluding Florida, New York Botanical Garden, New York, 1975). Collected from Lake Serene near Edmonds, Snohomish Co., Washington, in 1912 (C. L. Hitchock, A. Cronquist, M. Ownbey, and J. W. Thompson, Vascular plants of the Pacific Northwest, part 1: vascular cryptogams, gymnosperms, and monocotyledons, University of Washington Press, Seattle, 1969). We have been unable to locate vouchers for the collection in question.

Significance. The Silver Lake site is the only known extant population in the contiguous United States. The Lake Serene site is now urbanized and the population extinct. The species is listed as threatened (Washington State Natural Heritage Program, Endangered threatened & sensitive vascular plants of Washington, Department of Natural Resources, Olympia, 1990). The Silver Lake site is further inland and at higher elevation than locations reported from British Columbia, where it generally

occurs in coastal forests (R. L. Taylor and B. MacBride, Vascular plants of British Columbia, University of British Columbia Press, Vancouver, 1977).

—ALBERT E. GRABLE, 630 SW 3rd St., College Place WA 99324; JOSEPH E. LAFERRIÈRE, Marion Ownbey Herbarium, Washington State University, Pullman WA 99164-4309.

REVIEW

Oaks of California. By BRUCE PAVLIK, PAMELA C. MUICK, SHARON JOHNSON, and MARJORIE POPPER. 1991. Cachuma Press, Los Olivos, CA, and The California Oaks Foundation. 184 pp. $19.95 Paper, $29.95 Cloth.

Oaks of California, written by Bruce Pavlik and collaborators, is unique in its wide appeal to both specialists as well as enthusiasts. Obscure yet captivating details invite exploration into the world of oaks while providing depth to match the book's substantial ecological and historical breadth. Unusually beautiful graphics along with contemporary and artifactual details make *Oaks of California* a visually appealing collector's item as well.

Pavlik has produced a thorough, well-communicated, enjoyable monograph beginning with the botanical basics. These include definitions, the taxonomy of the genus *Quercus,* descriptions and profiles of each species as well as discussions of hybrid crosses. Identification is significantly enhanced by watercolors by Allison Atwill and abundant colorful photographs. Ecological issues covering geographical distribution, range maps, geological associations, and oak-aligned plant communities receive well organized, detailed emphases also.

The chapter entitled, "Oaks and Wildlife" is devoted to the intricate dynamic between oaks and literally thousands of organisms. Specifically described are oak-engendered relationships and dependencies of insects, mammals, reptiles and birds. For example, the commentary on the interplay between the host oaks and parasitic gall wasps which are further preyed upon by other insects suggests the centrality and importance of this genus to California's biota.

"California Oaks and the Human Past" then provides fascinating anthropological evidence of the monumental role these majestic trees played in the survival and sanctity of early Americans. Reliance of humans upon oaks for food, medicine, shelter, arts and ceremony was total. Pavlik tells of later societies' unfortunate lack of regard towards California's heritage trees and the decimation which was to follow.

Chapter by chapter, Pavlik and co-authors lead the reader to the unquestionable conclusion that the genus *Quercus,* once integral to all forms of life within the state, now requires active protection. Leaving little up to the imagination, methods of recently successful oak woodland conservation attempts have been documented to assist in today's badly needed efforts.

The final reference chapters are no less pertinent. From recommendations on statewide preserves or the locations of unique oak woodland habitats, to indexes of common and scientific names of plants, invertebrates, vertebrates noted in the text, to a listing of "Endangered Species Associated with California Oaks", each list will provide critical information to any biologist.

Ever depiction, and every articulately expressed thought in *Oaks of California* reminds the reader of the precious oak-peppered retreats under which each of us has at one time or another sought refuge and inspiration. This book will act not only as educator, but as activator in the on-going challenge for the preservation of California native oaks.

MELANIE BAER-KEELEY, Matilija Nursery, Malibu, CA 90265.

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CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

DANTHONIA ANNABLEAE (POACEAE: DANTHONIEAE), A NEW SPECIES FROM BOLIVIA

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Abstract

Danthonia annableae from Bolivia is described and illustrated. The new species is distinguished by possessing lemmas with acute or obtuse lateral lobes that are not prolonged into seta, few-flowered panicles with one or occasionally two spikelets, and the presence of cleistogamous and chasmogamous florets in the aerial spikelets. A tabular comparison with *D. chilensis* and *D. cirrata* is given.

Resumen

Danthonia annableae de Bolivia, se describe e ilustra. La nueva especie se distingue por poseer lemmas con lóbulos laterales agudo u obtusos, no prolongados en setas, panojas pauciespiculadas con una o dos espiguillas, y la presencia de flores cleistógamas y casmogamas en espiguillas aéreas. Se presenta una tabla comparativa con *D. chilensis* y *D. cirrata.*

The genus *Danthonia* DC. in Lam. & DC., s.l. comprises well over 100 named species distributed throughout both hemispheres (Conert 1971; Tomlinson 1985). More recently the genus has been interpreted in a narrow sense and perhaps contains 20 species located in Europe, North, and South America (Clayton and Renvoize 1986). The generic concepts in Danthonieae are highly controversial and relationships with *Chionochloa* Zotov, *Karrochloa* Conert & Türpe, *Merxmuellera* Conert, *Notodanthonia* Zotov, *Pseudopentameris* Conert, and *Rytidosperma* Steud. have been indicated (Clayton and Renvoize 1986; Connor 1986; Connor and Edgar 1979; Conert 1970, 1971, 1975a, b, 1983; Conert and Türpe 1969; Nicora 1978; P. V. dos Santos and Boechat 1989; Tomlinson 1985; Vickery 1956; Zotov 1963). Species of *Danthonia* s.s. are characterized by having hairy (but not in tufts) or glabrous, bilobed lemmas with a geniculate awn arising between the lobes, glabrous lodicules, and short ciliate ligules (Clayton and Renvoize 1986).

The new species is named after Carol Ruth Annable who first brought this enigmatic grass to my attention on our recent collecting trip in Bolivia.
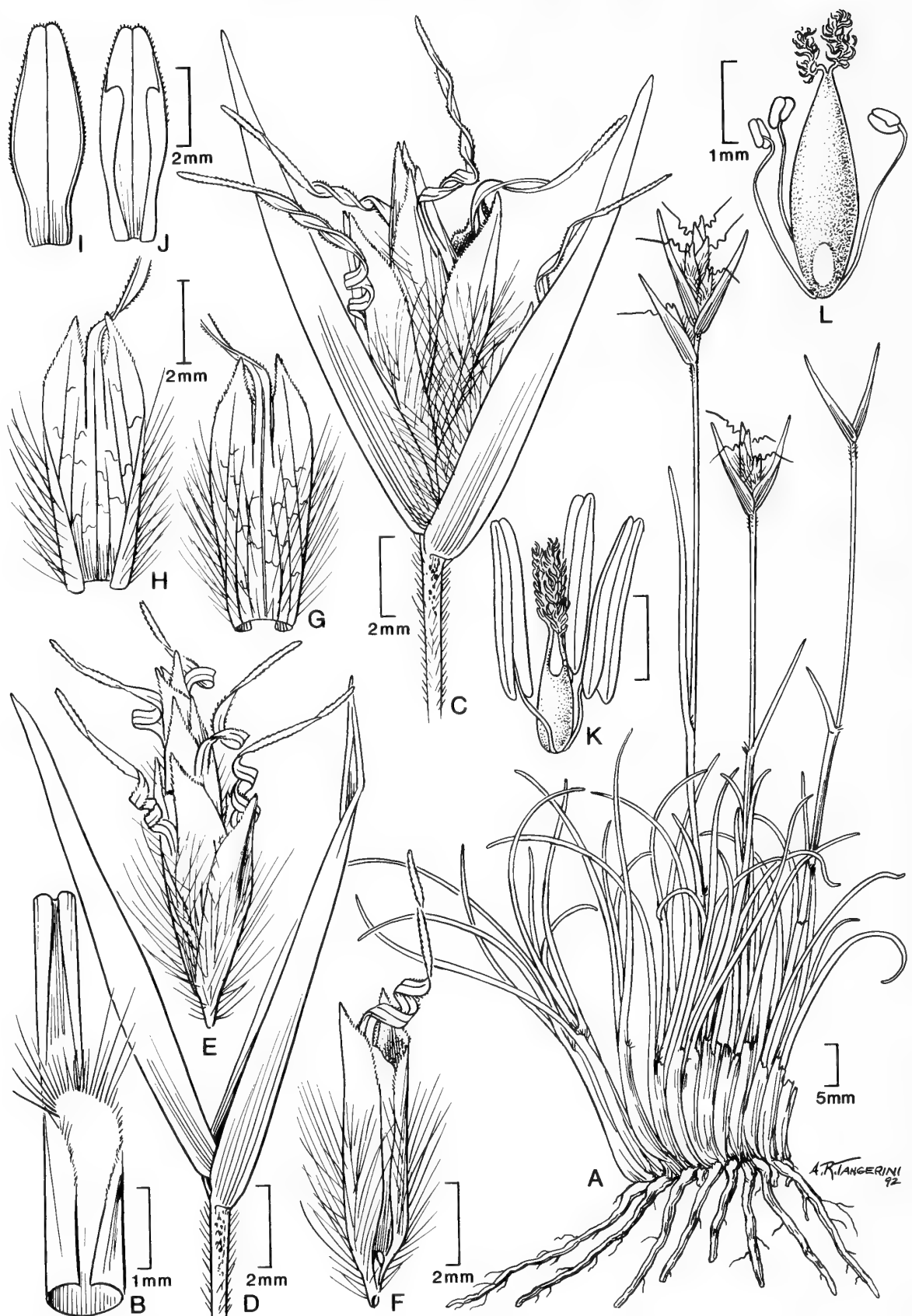
FIG. 1. *Danthonia annableae*, Potosi, Bolivia (*Peterson and Annable 11832*). A. Habit. B. Ligule. C. Spikelet. D. Glumes. E. Florets. F. Floret. G. Lemma, dorsal view. H. Lemma, ventral view. I. Palea, dorsal view. J. Palea, ventral view. K. Pistil and stamens from a chasmogamons floret. L. Caryopsis and stamens from a cleisto-gamons floret.

Danthonia annableae P.M. Peterson & Rúgolo, sp. nov. (Fig. 1).—
TYPE: BOLIVIA, Potosí, approximately 18 km NW of Salo on
road to Atocha, 21°10′S, 65°58′W, 21 Mar 1992, *Peterson and
Annable 11832* (holotype, SI; isotypes, FR, K, LPB, MO, TAES,
US).

A *Danthonia cirrata* culmis 2–12 cm altis; laminis 0.7–5 cm longis,
0.4–0.6 mm lata, involuta arcte; paniculis 1–2 cm longis cum 1 vel
2 spiculis, 4–6 florae cleistogamus vel chasmogamus; glumis 0.95–
1.6 cm longis; lobis lateralis acutis vel obtusis, sine seta, lemmatum
5.5–7.6 mm longorum, recedit.

Densely caespitose perennials. Culms 2–12 cm tall, erect, often
connected below by an extremely short rhizome, forming a linear
row of stems; mostly glabrous below the nodes (one per culm) oc-
casionally with a few scattered hairs and somewhat finely red-dotted;
internodes 0.6–6 cm long, glabrous. Sheaths 0.2–3.5 cm long, about
½ as long as the internode, turning papery and light brownish below,
glabrous, hairy near the summit, the hairs 0.8–1.6 mm long; margins
hyaline. Ligules 0.4–0.8 mm long, a dense ring of short hairs, the
hairs longer at the sides and up to 2.5 mm long. Blades 0.7–5 cm
long, 0.4–0.6 mm wide, tightly involute, filiform, arcuate upon dry-
ing, glabrous with an occasional long stiff hair below, the hairs 0.6–
1.2 mm long and glabrous to scaberulous above; apex acute, navic-
ular. Panicles 1–2 cm long, 0.5–1 cm wide, much reduced to one or
occasionally two spikelets; pedicels of the terminal spikelets 2–5 mm
long, pilose, the lower spikelets usually sessile. Spikelets 4–6-flow-
ered, erect to slightly reflexed, the segments of the rachilla 0.5–1.4
mm long, densely pilose. Glumes 0.95–1.6 cm long, narrowly lan-
ceolate, prominently 3-nerved, glabrous, about equal in length and
twice as long as the lower lemma, exceeding the florets, the center
area between the outer nerves greenish, the wide margins hyaline;
apex long acuminate. Lemmas 5.5–7.6 mm long (including lateral
lobes), oblong-elliptic, membranous, greenish, 7–9-nerved, the nerves
sometimes indistinct, loosely pilose along lower ⅔, margins hyaline
and more densely pilose, the hairs 1–2.3 mm long; callus about 1–
1.4 mm long, thinly indurated and short pilose; apex with two lateral
lobes 1–3 mm long, apex acute to obtuse and minutely ciliolate along
the tip; the sinus with a flattened awn 5–10 mm long, geniculate
above and twisted near the base, yellowish below and purplish above.
Paleas 5.4–6.8 mm long, elliptic, 2-nerved, strongly keeled, hyaline,
firm and minutely ciliolate on the keels; apex truncate to obtuse,
sometimes obscurely emarginate, minutely ciliolate. Two lodicules
0.3–0.5 mm long, cuneate, glabrous. Stamens 3, anthers 1.8–2.5 mm
long, yellowish-purple. Caryopses 2–2.4 mm long, elliptic, yellowish
brown, the hilum ⅓ the length of the caryopsis. Cleistogamous florets
present in the aerial spikelets with smaller, bisporangiate anthers

TABLE 1. SALIENT CHARACTERS DISTINGUISHING (*DANTHONIA ANNABLEAE, D. CHILENSIS,* AND *D. CIRRATA.*

Characters	*D. annableae*	*D. chilensis*	*D. cirrata*
Culm height (cm)	2–12	15–40	(10)20–85
Blade	tightly involute	flat/involute	flat/folded rarely involute
Blade length (cm)	0.7–5	5–12	3–22
Blade width (mm)	0.4–0.6	0.8–1.2	1–3
Spikelets per panicle	1 or 2	2–6	(2)3–35
Florets per spikelet	4–6	3–5	5–10
Panicle length (cm)	1–2	2.5–3.5	3–12
Glume length (mm)	9.5–16	10–12	10–25
Shape of lemmatal lateral lobes	acute	acuminate	acuminate
Lemmatal lateral lobes with seta	absent	present	present
Lemma hairs (dorsal surface)	present	absent	present
Palea shape	elliptic	obovate	elliptic

0.2–0.5 mm long, usually lacking lodicules. Chromosome number unknown.

HABITAT, ANATOMY, AND RELATIONSHIPS

Danthonia annableae is known only from the type locality, northwest of Tupiza on the road towards Atocha and Uyuni. It occurs in association with species of *Piptochaetium* Presl, *Festuca* L., and *Ephedra* L. on yellowish-brown shale barrens at 3900 m. The morphological characters that can consistently be used to distinguish among *D. annableae, D. chilensis* Desv., and *D. cirrata* are listed in Table 1. *Danthonia annableae* differs from the latter two species by possessing lemmas with acute to obtuse lateral lobes that are not prolonged into seta, few-flowered panicles with one or occasionally two spikelets, and the presence of cleistogamous and chasmogamous florets in the aerial spikelets.

The leaf blades in transection possess narrow and steep sided adaxial furrows and rounded adaxial ribs similar to other species in the genus. However, the outer bundle sheaths of the secondary and tertiary vascular bundles are usually complete and only the primary vascular bundles are adaxially incomplete. In the primary vascular bundles the phloem is not divided into two equal groups as in *D. cirrata* Hack. & Arech., *D. malacantha* (Steud.) Pilger and *D. montana* Doell (Tomlinson 1985). Adaxial sclerenchyma is associated with all vascular bundles (lacking in *D. chaseana* Conert, *D. cirrata,*

and occasionally *D. sericea* Nutt.) and there is no bundle sheath extension of colorless cells (Tomlinson 1985).

The new species seems most clearly related to *D. cirrata*, a wide ranging taxon predominantly from lower elevations (less than 1500 m) grasslands of Santa Catarina (Smith et al. 1982), the Rio Grande do Sul (P. V. dos Santos and Boechat 1989), Brazil, Uruguay (Rosengurtt and Arrillaga de Maffei 1963), and Argentina (Nicora 1978). However a specimen of *D. cirrata* [*Beck, Gomez, and L. Rugolo 18103* (SI)] from Departamento Cochabamba, Bolivia was collected at 3200 m. *Danthonia annableae* can be separated from *D. cirrata* by having shorter culms, more tightly involute and smaller leaf blades (width and length), shorter panicle with less spikelets (1 or 2), only 4–6 florets per spikelet, shorter glumes, and lemmas with acute rather than acuminate lateral lobes without apical seta.

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ISOZYME VARIATION, ECOLOGY AND PHYTOGEOGRAPHY OF *ANTENNARIA SOLICEPS* (ASTERACEAE: INULEAE), AN ALPINE APOMICT FROM THE SPRING MOUNTAINS, NEVADA

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Abstract

Antennaria soliceps Blake is a narrow endemic, known only from a small area of the Spring Mountains, Clark County, southern Nevada. The Spring Mountains are an isolated biome harboring many endemics, including *A. soliceps*. Populations of *A. soliceps* are found on a limestone talus ridge, which extends both above and below treeline for six km east southeast of Charleston Peak. This duodecaploid species is gynoecious, and reproduction is achieved through agamospermy and stoloniferous growth. Enzyme electrophoresis was used to assess the genetic diversity of five populations surveyed at one-mile intervals along the ridge. It appears that *A. soliceps* possesses only one electrophoretic genotype and, therefore, is a single genetic individual. *Antennaria soliceps* is hypothesized to be related to *A. aromatica* on the basis of habitat and morphological characteristics and to *A. parvifolia* on the basis of cytological and other morphological features. Establishment of *A. soliceps* probably occurred in the Pleistocene during which moister and cooler conditions allowed the migration of northern plant taxa to this area.

The Spring Mountains of southern Nevada are an isolated range occurring at the southern edge of the Great Basin. Clokey (1951), author of the first and only flora of the range, referred to them as the Charleston Mountains. Charleston Peak is the only summit of the range that rises above treeline. The range is surrounded by desert which acts as a barrier to alpine plant migration between mountain ranges in the Great Basin (Harper et al. 1978). The isolation of the alpine peaks of the Spring Mountains provided a unique environment in which several insular endemics evolved, including *Antennaria soliceps*.

Antennaria soliceps is a perennial herb characterized by a monocephalous flowering stalk and a cushion plant growth form. Its six-kilometer long range is restricted to the talus areas of a ridge, composed entirely of Mississippian limestone (Clokey 1951), both above and below treeline between Griffith and Charleston Peaks (Fig. 1). Although the genus is dioecious, only pistillate plants of *A. soliceps* are known to exist. As in other gynoecious species of *Antennaria* (Bayer 1990b), reproduction in *A. soliceps* involves gametophytic apomixis, as well as vegetative asexuality via stolons, resulting in the production of progeny that are genetically identical to the ma-

ternal individuals. Thus, a low level of genetic diversity might be expected in the species. *Antennaria soliceps* has a very high ploidal level, and although an exact chromosome number has been elusive due to the high number of chromosomes, it has been observed that $2n$=ca. 168, making the species a duodecaploid (Bayer unpublished data) based on $x = 14$. This is the highest ploidal level recorded for any species of *Antennaria*.

Determining the origin of *A. soliceps* is problematical, as has been determining the phylogenetic relationships of several of the other high elevation endemics of the Spring Mountains, such as *Ivesia cryptocaulis* and *Tanacetum compactum* (Clokey 1951). In his protologue, Blake (1938) stated that *A. soliceps* belonged to the "*A. media* group", but was unique in possessing single large heads. Later authors (Clokey 1951; Knight 1990) echoed Blake's (1938) statements on the relationship. As in other agamic complexes, it is well documented that asexual *Antennaria* species are derived from sexual species (Bayer 1987), therefore we must look to a sexual species for the parents of *A. soliceps*. *Antennaria media* Greene and *A. pulchella* Greene (the diploid parent of *A. media*) resemble *A. soliceps* in being alpine plants with dark black or brown colored phyllaries, but they are polycephalous, do not develop the dense cushion plant growth form, and are not confined edaphically to limestone substrates (Bayer 1990a). Their leaf shape is linear-spathulate rather than cuneate-spathulate as in *A. soliceps*. However, *A. aromatica* Evert, a recently described (Evert 1984) sexual species from Montana and Wyoming, and *A. parvifolia* Nutt. (=*A. aprica* Greene sensu Clokey 1951) are two species that possess morphological, cytological, and ecological features that implicate them as the possible progenitors of *A. soliceps*. No other sexual species of *Antennaria* possesses characteristics that would involve them in the parentage of *A. soliceps*.

With the increased interest in genetic diversity of geographically restricted endemics and their conservation (Karron 1987), as well as the increased interest in genetic variation in clonal organisms (Ellstrand and Roose 1987), it seemed appropriate to investigate the genetic diversity in *A. soliceps*. An electrophoretic survey was therefore undertaken to determine genetic (clonal) diversity in this geographically restricted endemic. The study also discusses the origin and phytogeographic history of *A. soliceps* through morphological and ecological comparisons.

Methods

Location of sites and sampling. Antennaria soliceps occurs in scattered populations ranging from a few individuals to many hundred individuals. The Spring Mountains have been extensively botanized by well-known collectors, including Clokey, Alexander and Kellogg,
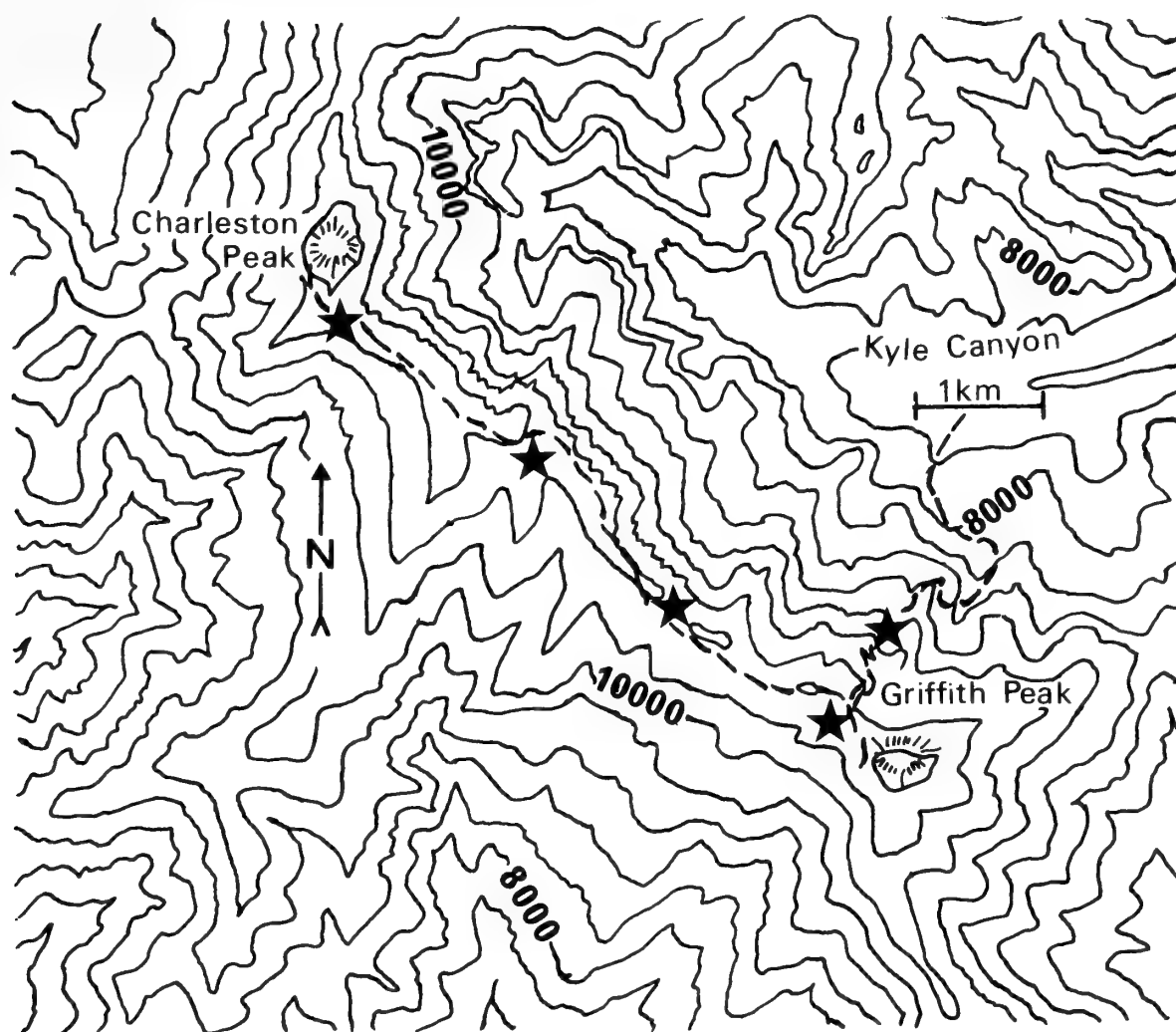
FIG. 1.   Topographic map of the Charleston Peaks portion of the Spring Mountains, Clark Co., Nevada (contour interval = 400 ft). A prominent feature is the ridge extending between Griffith Peak (11,072′) and Charleston Peak (11,918′). Kyle Canyon is the location of the trailhead (7600′) of the "south loop" trail (dotted line). Populations of *A. soliceps* that were sampled (stars) occurred near treeline at elevations from 10,000′ to 11,150′ (3200–3400 m). Population identifications are from left (west) to right (on the north slope of Griffith Peak): NV-90020, NV-90019, NV-90018, NV-90017, and NV-700. Only sites NV-90020 and NV-90019 are truly alpine. Voucher specimens are at ALTA.

Train, Jones, Heller, Tidestrom, Hitchcock, and Jaeger among others (Clokey 1951) during the past 70 years, yet no additional sites for *A. soliceps* have ever been discovered. Recent explorations, targeting conservation of the species, have not uncovered any new sites (Knight 1990; T. Knight personal communication). In this study, four relatively large populations, covering the entire known range of the species, were sampled at equal intervals (about 1 mile apart) along the isolated ridge where *A. soliceps* occurs (Fig. 1). In addition, one rather ecologically atypical population, which occurs in the forest of bristlecone pine on the slope above Kyle Canyon, was also located and sampled (Fig. 1). Small portions of clones (ramets) were sampled at random and excavated for cultivation in the greenhouse.

Population genetics. Gel electrophoresis was carried out on 108 individuals from the five populations to determine the genetic diversity of the species. Nine enzyme systems were assayed: esterase (EST), glutamate oxaloacetate transaminase (GOT), leucine aminopeptidase (LAP), phosphoglucose isomerase (PGI), triosephosphate isomerase (TPI), acid phosphatase (ACP), malate dehydrogenase (MDH), phosphoglucomutase (PGM), and shikimic dehydrogenase (SKDH). Enzymes for assay were obtained from young leaves ground in cold Tris-HCl grinding buffer: 0.1 M Tris-HCl, pH 7.5, 4.0 mM 2-mercaptoethanol, 1.0 mM EDTA (disodium salt), 0.2 M sucrose, 0.6% polyvinyl-polypyrrolidone (5:1 ratio of 40K: 360K m.w.), 2.0% PEG (8K m.w.), 0.1% BSA, and 0.002 M ascorbic acid. These extracts were then absorbed onto filter paper wicks and stored at $-20°C$ overnight. The next day the wicks were loaded onto 12% starch gels and subsequently assayed for the above-mentioned nine enzyme systems. ACP, MDH, PGM, and SKDH were all observed using the same buffer system: the electrode buffer consisted of 0.007 M citric acid·H_2O and 0.065 M L-histidine (free base), and the gel buffer of 0.002 M citric acid·H_2O (pH 6.5) and 0.015 M L-histidine (free base) (Cardy et al. 1981). EST, GOT, LAP, PGI, and TPI were resolved using 0.038 M lithium hydroxide·H_2O–0.188 M boric acid (pH 8.3) as an electrode buffer and a gel buffer composed of 1 part 0.038 M lithium hydroxide·H_2O–0.188 M boric acid (pH 8.3), and 9 parts of 0.045 M Tris–0.007 citric acid (pH 8.4) (Soltis et al. 1983). The protocols described by Soltis et al. (1983) were used for staining the gels for each enzyme system.

The genetic basis of the isozyme banding patterns cannot be determined because of the high ploidal level of this taxon. Specifically, allelic frequencies for polymorphic loci lead to a large number of possible types of unbalanced heterozygotes, which cannot be visually differentiated in the gels [see Bayer (1989a) for a discussion of the problems associated with multisomic inheritance in *Antennaria*]. Therefore, a simple comparison of the banding patterns was carried out, and inferences were made based on the degree of similarity. Intensity of allozyme activity, banding patterns, and enzyme migration were characteristics on which the comparisons were based. Isozymes cannot be used to evaluate the origin of *A. soliceps* because of the uncertainty of genetic interpretation of the bands and because two possible parents, *A. aromatica* and *A. media,* do not have diagnostic alleles that can be used to confirm their presence in polyploid derivatives (Bayer 1989c). The isozymes of *A. parvifolia* have not been investigated, but high ploidy in this species complex would also hinder interpretation of the banding patterns, making use of isozymes as genetic markers difficult.

Ecology and morphology. An ecological study of *A. soliceps* was carried out using data on both the environment and community associates to compare the habitat of this species with one of its putative progenitors, *A. aromatica,* with which it appears to be very similar edaphically. Documentation of a similarity in habitat between the two species would lend additional support to our hypothesis that the two are a progenitor-derivative species pair. The methods were basically the same as those outlined in an earlier study (Bayer et al. 1991) and the data for habitats of *A. aromatica* were extracted from that earlier data set. At each *A. soliceps* study site, elevation above sea level (meters) and slope (degrees) were measured using a calibrated barometer and clinometer, respectively. Soil temperature difference (°C) between the surface and 10 cm depth, and soil unconfined strength (kg/cm^2), measured by a soil penetrometer, were recorded. This gives a measure of the insulating/temperature retention capacity of the soil.

Soil samples were collected from each of the five study sites, allowed to air dry, and subjected to chemical analysis by the soil analysis laboratory at the Northern Alberta Forestry Center, Edmonton. The macro- and micronutrients measured include extractable forms of calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), phosphorus (PO$_4$), potassium (K), sodium (Na), sulfur (SO$_4$), and zinc (Zn) measured in mg/kg. Nitrogen was not determined, as the amount of this nutrient often varies between the time the soil is collected and the time of analysis. The percent organic matter and pH of the soil were also determined. Herbarium specimens of all community associates were also collected from each site and were identified using taxonomic keys in Clokey (1951). The nomenclature (Table 1) follows Clokey (1951), as more recent floristic treatments do not exist for southern Nevada.

Ordination of nominal species data and environmental variables from thirteen study sites (five of *A. soliceps* and eight of *A. aromatica*) was carried out using the canonical correspondence analysis (CCA) option of the Canonical Community Ordination (CANOCO) program (ter Braak 1985). This method of analysis allows the environmental variables to be related to species data simultaneously and is becoming the preferred ordination method for the analysis of data used in vegetation classification (ter Braak 1986, 1987, 1988; John 1989; Gignac and Vitt 1990; Bayer et al. 1991). The program was run without any transformation of the variables, weighting environmental variables, or axis rescaling. In this study, the ordination was performed to determine and visualize the habitat and species associates for the two *Antennaria* species.

Gross morphological comparisons among species of *Antennaria*

TABLE 1. COMMUNITY ASSOCIATES FROM FIVE SITES CONTAINING POPULATIONS OF *ANTENNARIA SOLICEPS*. Presented are taxon names arranged alphabetically by genus and occurrence (+ = present; − = absent) at each of the sites; 07 = NV-700, 17 = NV-90017, 18 = NV-90018, 19 = NV-90019, 20 = NV-90020; * = endemic to Clark Co., Nevada (Spring Mountains and adjacent Sheep Range, ** = endemic to the Spring Mountains, *** = narrowly endemic to the Charleston Peak area and ridges extending from it. All other taxa are more widespread in North America.

	Sites				
Taxa	07	17	18	19	20
Actinea lemmonii (Greene) Blake	−	+	+	+	−
Antennaria soliceps Blake***	+	+	+	+	+
Aquilegia scopulorum Tidestr.	−	+	−	−	−
Artemisia michauxiana Besser	−	+	−	−	−
Astragalus mancus (Rydb.) Wheeler	−	+	+	−	−
Astragalus platytropis Gray	−	−	−	−	+
Crepis nana Richards.	−	−	−	−	+
Cystopteris fragilis (L.) Bernh.	+	−	−	−	−
Dodecatheon jeffreyi Moore var. *redolens* Hall	−	−	−	+	−
Draba jaegeri Munz & Johnston *in* Munz***	−	−	−	+	+
Erigeron clokeyi Cronquist	−	+	+	+	+
Erysimum capitata (Dougl.) Greene	+	−	−	−	−
Festuca ovina L. var. *brachyphylla* (Schult.) Hall	−	−	−	+	−
Gutierrezia sarothrae (Pursh) Britton & Rusby	−	+	−	−	−
Ivesia cryptocaulis (Clokey) Keck***	−	−	−	+	+
Jamesia americana Torr. & Gray	+	−	−	−	−
Lesquerella hitchcockii Munz*	−	+	−	+	+
Lupinus alpestris A. Nels.	+	−	−	−	−
Oenothera caespitosa Nutt. var. *crinata* (Rydb.) Munz	−	−	−	−	+
Oxytropis oreophila Gray	−	+	−	+	+
Pedicularis semibarbata Gray ssp. *charlestonensis* (Pennell & Clokey) Clokey*	+	−	+	−	−
Penstemon keckii Clokey**	+	−	−	−	−
Physaria chambersii Rollins	+	−	−	−	−
Pinus longaeva D. K. Bailey (*P. aristata* of Clokey)	+	+	+	+	−
Poa secunda Presl.	−	−	+	−	−
Potentilla beanii Clokey***	−	+	+	−	−
Ribes montigenum McClatchie	−	−	−	+	−
Sitanion hystrix (Nutt.) Smith	−	+	−	+	+
Tanacetum compactum Hall***	−	−	−	+	+
Trisetum spicatum (L.) Richt.	−	−	+	−	−
Valeriana puberulenta Rydb.	+	−	−	−	−

were based on examination of herbarium material at ALTA and cultivated living material.

RESULTS

All nine enzyme systems produced favorable enzyme activity and good resolution. Variation among the 108 individuals assayed was

FIG. 2.   Gross morphological comparison of *Antennaria parvifolia* (left), *A. soliceps* (center) and *A. aromatica* (right). These pistillate specimens are from populations CO-90053, NV-90020, and M-628 for *A. parvifolia, A. soliceps* and *A. aromatica,* respectively. Vouchers at ALTA.

absent, as banding patterns and staining intensity were identical in all individuals for the nine enzyme systems.

Antennaria soliceps and *A. aromatica* have similar morphology. The overall size of the plants (Fig. 2) is similar as is their cushion plant growth form. Leaf size, shape, and spacing on the short stolons are similar in both species (Fig. 2). Head size is somewhat comparable, but with respect to head number per stem *A. aromatica* is pleiocephalous and *A. soliceps* usually monocephalous (Fig. 2). Both possess brown or green-based phyllaries with white or brown at the tips. The typical habitat of *A. soliceps* is calcareous talus at an elevation equal to or above treeline, as is that of *A. aromatica* (Bayer 1989b). The comparisons of gross morphological features between *A. soliceps* and *A. aromatica* (Fig. 2) suggest that the two species are closely related and that *A. aromatica* may be a parental species of *A. soliceps.* In its large head size and more spathulate leaf shape, *A. soliceps* also resembles *A. parvifolia,* whose sexual phase still occurs on montane slopes in the Spring Mountains at elevations up to 3150 m.

In the ordination diagram (Fig. 3), the lines representing environmental variables point in the direction of maximum change in the variable, and the length of the line indicates a relative measure of the rate of change in that variable (ter Braak 1987). Therefore, longer lines, especially those that extend to the margin of the graph, are more important parameters than short ones and tend to be more closely related to the patterns of community variation (ter Braak 1987). The relative position of each *Antennaria* species site or each community associate can best be viewed by projecting the points onto the lines. This is accomplished by first extending each line,
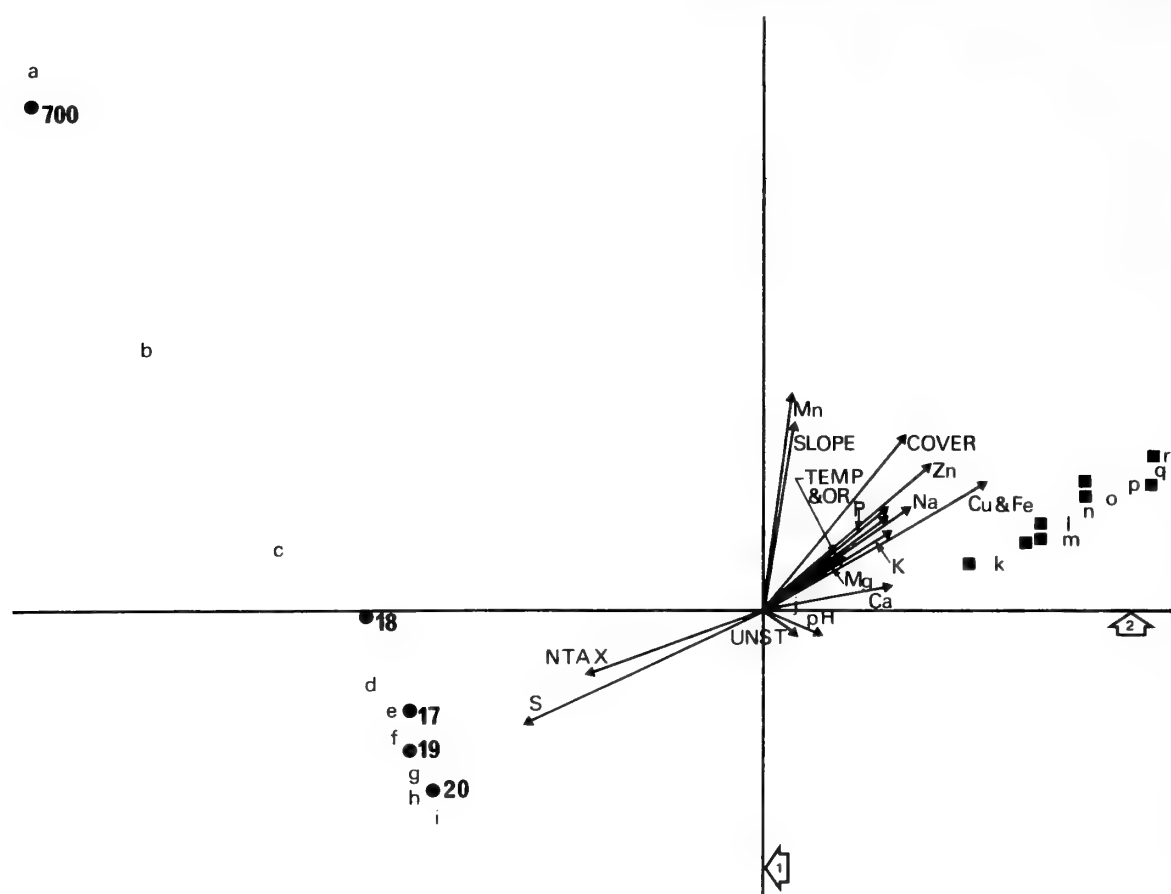
Fig. 3. The distribution of five study sites of *Antennaria soliceps* (solid circles) and eight of *A. aromatica* (solid squares) along CCA ordination axes 1 and 2 with environmental variables indicated by arrows. See text for guidance in interpretation of this diagram. Environmental factor abbreviations are as follows: Extractable forms of calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), phosphorus (P), potassium (K), sodium (Na), sulfur (S) and zinc (Zn) and percent organic matter (OR), soil temp (TEMP), percent cover (COVER), slope (SLOPE), pH (pH), number of taxa at each site (NTAX), and soil unconfined strength (UNST). Site abbreviations for *A. soliceps* are NV-700 (700), NV-90017 (17), NV-90018 (18), NV-90019 (19), and NV-90020 (20). Community associates are represented on the ordination axes as lower case letters. Several species may be represented by one letter and abbreviations are as follows: a = *Cystopteris fragilis, Erysimum capitata, Jamesia americana, Lupinus alpestris, Penstemon keckii, Physaria chambersii,* and *Valeriana puberulenta,* b = *Pedicularis semibarbata* ssp. *charlestonensis,* c = *Pinus longaeva,* d = *Astragalus mancus* and *Potentilla beanii,* e = *Actinea lemmonii,* f = *Aquilegia scopulorum, Artemisia michauxiana, Erigeron clokeyi* and *Gutierrezia sarothrae,* g = *Dodecatheon jeffreyi* var. *redolens, Lesquerella hitchcockii, Oxytropis oreophila,* and *Ribes montigenum,* h = *Draba jaegeri, Ivesia cryptocaulis,* and *Tanacetum compactum,* i = *Astragalus platytropis, Crepis nana* and *Oenothera caespitosa* var. *crinata,* j = grasses, k = *Paronychia sessiliflora, Pteryxia hendersonii,* and *Ribes inerme,* l = *Antennaria umbrinella* and *Astragalus alpinus,* m = *Androsace chamaejasme, Arcostaphylos uvi-ursi, Dryas octopetala, Hedysarum alpinum, Valeriana edulis, Astragalus aboriginum* and *Oxytropis campestris,* n = *Potentilla pensylvanica* and *Zygadenus elegans,* o = *Pentaphylloides floribunda, Erigeron ochroleucus, Lupinus argenteus, Oxytropis splendens, Silene acaulis, Geum rossii* and *Minuartia obtusiloba,* p = *Senecio canus, Phlox caespitosa* and *Anemone multifida,* q = *Bupleurum americanum, Draba oligosperma, Eritrichium nanum* and *Hymenoxys acaulis,* r = *Ivesia gordonii* and *Penstemon attenuatus.*

TABLE 2. SOIL COMPOSITION AND ENVIRONMENTAL VARIABLES FROM FIVE SITES CONTAINING *ANTENNARIA SOLICEPS*. Presented are minerals, percentage organic matter, pH, soil temperature difference between the surface and 10 cm depth (STEMP), unconfined soil strength (UNSTR), slope and percentage cover. Site abbreviations: 07 = NV-700, 17 = NV-90017, 18 = NV-90018, 19 = NV-90019, 20 = NV-90020.

Soil/plant components	Sites				
	07	17	18	19	20
Calcium (mg/kg)	254.2	355.9	614.8	516.3	588.6
Copper (mg/kg)	0.07	0.09	0.45	0.06	0.25
Iron (mg/kg)	0.9	0.11	0.84	0.30	0.47
Magnesium (mg/kg)	56.83	91.17	293.6	131.0	134.0
Manganese (mg/kg)	13.21	5.56	7.46	4.29	2.80
Phosphorus (mg/kg)	1.11	0.73	1.02	1.47	2.07
Potassium (mg/kg)	115.2	103.4	184.2	111.2	135.5
Sodium (mg/kg)	5.29	7.60	15.61	10.48	15.70
Sulfur (mg/kg)	18.99	23.87	52.80	40.18	53.18
Zinc (mg/kg)	0.45	0.01	0.01	0.01	0.01
Organic matter (%)	2.48	1.90	4.87	1.69	4.49
pH	6.9	7.28	7.56	7.46	7.55
STEMP (degrees C)	3.0	4.0	1.0	2.0	4.0
UNSTR (kg/cm^2)	1.50	1.75	1.5	2.0	2.5
Slope (degrees)	1.0	0.5	0.5	1.0	1.5
Percentage cover	30.0	20.0	25.0	18.0	18.0

either on paper or in the mind, in both directions to the edge of the diagram. Then draw or visualize a line from the site symbols, perpendicular to the line until it intersects the line. The ranking of those endpoints along the line is an approximate indication of the relative value of the weighted average of each species site with respect to that environmental variable. Also, the origin of the line indicates the grand mean, therefore if the endpoint of the line lies on the same side of the origin as the perpendicular intersect then that site has a weighted average that is higher than the grand average and vice-versa (ter Braak 1986). The raw environmental data are presented in Table 2.

From Figure 3 we can deduce that although *A. aromatica* and *A. soliceps* have distinct habitats, most of the environmental factors are not very different between their sites because the arrows are all relatively short in length. This is especially true if we compare these results to habitat differentiation between *A. aromatica* and other western North American species of *Antennaria* (Bayer et al. 1991), where all of the sexual taxa investigated differed by relatively large environmental differences. However, *A. aromatica* sites tend to differ from the *A. soliceps* sites by having relatively higher amounts of cover, zinc, sodium, copper, iron, and phosphorus in the soil and lower amounts of sulfur and numbers of species associates (NTAX) at the sites. Although copper, manganese, sulfur, and zinc may be

toxic to plants at certain pH values, it is unlikely that any of these nutrients affect the growth of the plants at the *A. soliceps* sites because the pH values of the soils are neutral to slightly alkaline and the amounts of all of these nutrients are at the low end of the range in amounts of these nutrients that are found in soils in general (Table 2). No community associates are shared by the two sets of sites, except the broad category of grasses (j), as might be expected due to the great phytogeographic distance that separates the range of the two species. The *A. aromatica* sites are all remarkably similar to each other and differ primarily by the above-mentioned environmental factors as well as having different species associates at each site (Fig. 3). The typical sites of *A. soliceps* that occur on the top of the ridge are also fairly similar to each other (Fig. 3). The atypical site (NV-700), which occurred well below treeline below site NV-90017, was quite different from the other sites (Fig. 3). Site NV-700 was most different from the other *A. soliceps* sites because it occurred on a slightly steeper slope with soil much higher in manganese than the other sites. Also this site had a completely different set of species associates including *Cystopteris fragilis, Erysimum capitata, Jamesia americana, Lupinus alpestris, Penstemon keckii, Physaria chambersii,* and *Valeriana puberulenta,* only sharing *Pedicularis semibarbata* and *Pinus longaeva* with the other sites (Fig. 3). Compared to edaphic conditions for other species of *Antennaria* (Bayer et al. 1991), *A. aromatica* and *A. soliceps* are more similar to each other than to other species of *Antennaria* because the sites of these species have gravelly soils, with high amounts of calcium, sulfur, and low manganese (Mn) and are found at high elevations in full sun.

DISCUSSION

Population genetics. A lack of genetic variation in the nine enzyme systems among 108 individuals strongly suggests that the entire species is a single genotype. This absence of genetic diversity is completely concordant with our supposition that *A. soliceps* is a gametophytic apomict, producing progeny that are genetically identical to the parental individuals. *Antennaria soliceps* thus apparently arose as a single pistillate individual that established itself on the Spring Mountains and reproduced apomictically. If more than one clone of *A. soliceps* did arise at the time of its origin, then its tiny geographic range could have resulted in the loss of all but one genotype. Consequently, the total lack of genetic variation within *A. soliceps* may be one explanation for its continued restricted range today, as there is no genetic variation that allows for individuals preadapted to slightly different environmental conditions to expand the range of the species. Additional explanations for its restricted range may relate to the dispersability of propagules to other suitable

habitats and their ease of establishment in those habitats. Because *A. soliceps* consists of a single genotype, its ability to survive changing climatic conditions will depend on the degree of phenotypic plasticity within this genotype.

Antennaria soliceps presents a somewhat unusual case when trying to compare its genetic population structure with that found in other plant species because it is not only a geographically restricted endemic, but is also an apomict. Karron (1987) summarized data on isozyme variation for widespread versus restricted congeneric species for all types of breeding systems, whereas Ellstrand and Roose (1987) reviewed that for clonal plants. Based on the data in these reviews it might be expected that a narrowly restricted agamospecies, such as *A. soliceps,* would have very small amounts of genetic variability and therefore it is not surprising to find that it is monoclonal. The only other species investigated thus far having a similar breeding system and somewhat narrow distribution is the gametophytic apomict, *Taraxacum obliquum* (Oostrum et al. 1985). No variation in genetic composition was detected in populations from the coast of the Netherlands, indicating that the populations were also monoclonal (Oostrum et al. 1985).

Phytogeography and evolution. The similarities between *A. aromatica* and *A. soliceps,* both the terms of morphology (Fig. 2) and habitat (Fig. 3), suggest it may be a parent. Growth form, leaf shape, phyllary color, and habitat are strikingly similar between the two taxa (Fig. 2). Unlike *A. aromatica, A. soliceps* is neither glandular nor aromatic, but neither are other apomicts thought to be derived from *A. aromatica* (Bayer 1989b). When *A. aromatica,* which occurs as a sexual species at diploid ($2n=28$) and tetraploid ($2n=56$) ploidal levels, is artificially hybridized with any other of a number of other sexual species of *Antennaria,* the resultant F_1 interspecific hybrids (vouchers at ALTA) are always non-glandular and odorless (Bayer unpublished data). Since most apomictic *Antennaria* are thought to be of allopolyploid (hybrid) origin (Bayer 1987), then *A. soliceps* is probably a hybrid between *A. aromatica* and some other sexual species of *Antennaria. Antennaria soliceps* also resembles *A. parvifolia* in its large head size and more spathulate leaf shape. Additional evidence in favor of *A. parvifolia* as contributing to the parentage of *A. soliceps* is cytological. *Antennaria soliceps* is high polyploid (ca. duodecaploid) and only in *A. parvifolia,* which occurs as a sexual species at tetraploid, hexaploid ($2n=84$), octoploid ($2n=112$) and decaploid ($2n=140$) ploidal levels, do ploidal levels approach that magnitude (Bayer and Stebbins 1987). The propensity for very high ploidal level in *A. soliceps* could have been inherited from *A. parvifolia.*
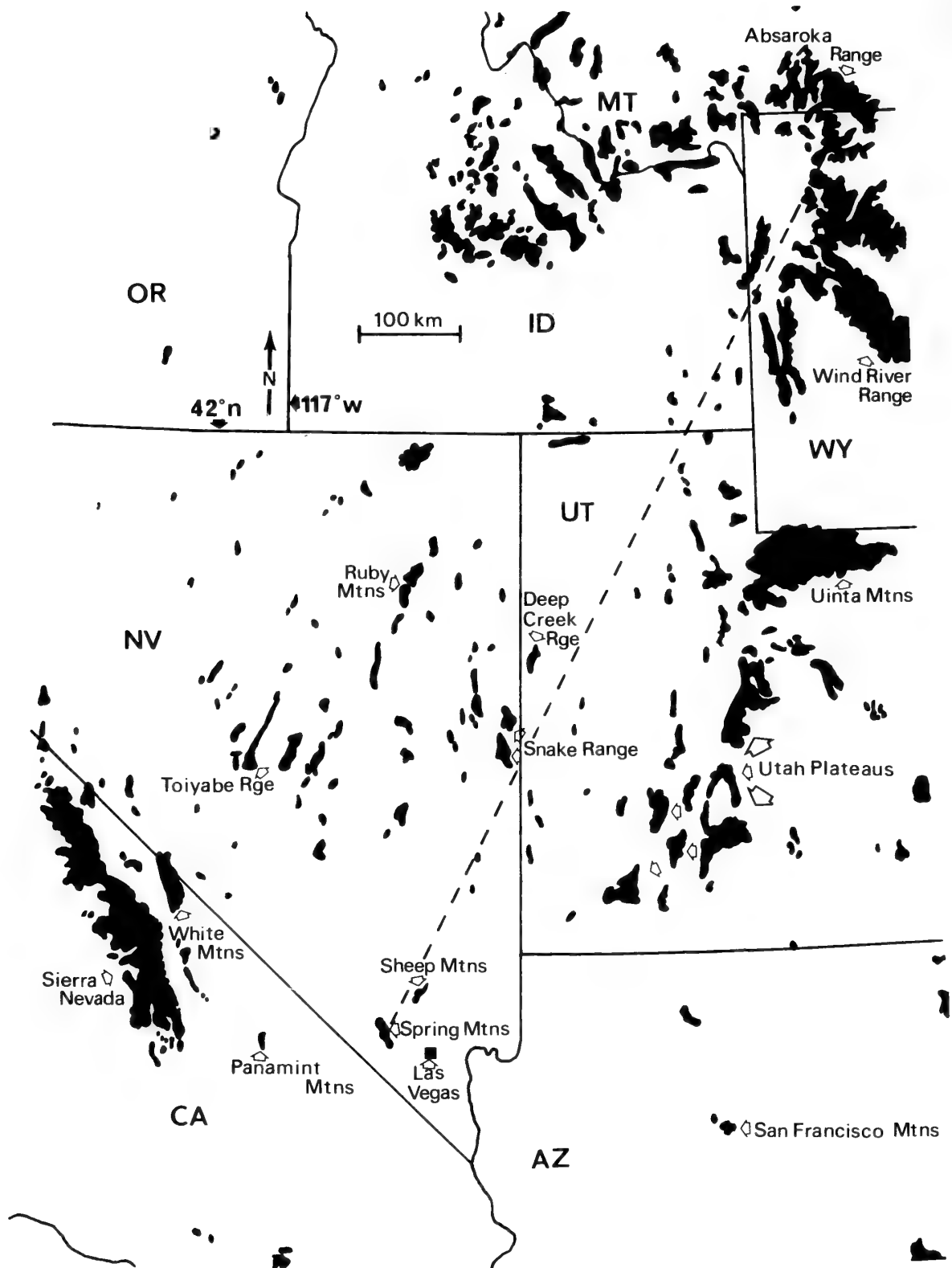
FIG. 4. Map of the Intermountain Region of the southwestern United States. *Antennaria soliceps* is endemic to the Spring Mountains. Areas in black are regions that are considered entirely or partially alpine at the present time (based on Billings 1978). Major mountain ranges are labeled. *Antennaria aromatic* occurs in the Absaroka Range, which is about 1000 km (dotted line) northeast of the Spring Mountains.

The flora of the Spring Mountains contains 12 endemics at high elevations from subalpine to alpine (Clokey 1951) and *A. soliceps* co-occurs with several of these including *Draba jaegeri, Ivesia cryptocaulis, Penstemon keckii, Potentilla beanii,* and *Tanacetum compactum* (Table 1). Billings (1978) has calculated an index of similarity between the Spring Mountains and other ranges of the Great Basin, Rockies and Sierra: Absaroka Range (8%), Deep Creek (13%), Ruby Mountains (8%), Toiyabe Range (18%), White Mountains (16%), Sierra Nevada (10%), and San Francisco Mountains (14%) (Fig. 4). Based on this, it is only about twice as likely that nearby mountain ranges (except the Ruby Mountains) are the source of the ancestors of *A. soliceps* as the distant northern Rockies (Beartooth Plateau; Absaroka Range) (Fig. 4). Also, overall the Rockies have had a much greater effect on the vascular plants species composition of mountains of the Great Basin than has the Sierra (Billings 1978). Additionally, the Rockies and Great Basin ranges have large areas of limestone talus habitat whereas the Sierra has very little (Billings 1978).

We offer the following phytogeographic hypothesis to account for the present day distributions of *A. aromatica* and *A. soliceps*. *Antennaria soliceps* may have established itself in the Spring Mountains during the Pleistocene when the continental climate was cooler and moister. During this epoch, the immediate area around the Spring Mountains was not desert as it is at present, rather there were many lakes and a diverse flora (Thompson and Mead 1982). Small glaciers existed on the peaks of the Spring Mountains creating cirques which now provide habitat for numerous endemics (Billings 1978). Alpine areas of Charleston Peak are much moister than the valley floor and lower slopes, but they are drier than comparable areas in the Rockies and Sierra Nevada because of the tremendous rainshadow provided by the Sierra (Billings 1978). Alpine habitat of the Charleston peak area was larger during the Quaternary (Fig. 4).

Perhaps *A. aromatica* expanded its range, during the Quaternary, towards the south and for a time occurred in southern Nevada (Fig. 4). Most of the ranges of eastern Nevada south of the Ruby Mountains are topped with calcareous rock, which could have provided "stepping stones" of suitable habitat for *A. aromatica* during the Pleistocene. If *A. aromatica* did occur in southern Nevada at that time, then it hybridized with another species of *Antennaria,* possibly *A. parvifolia,* giving rise to an asexual clone which established itself in the nearby mountains. As the climate became drier and warmer after the Pleistocene, this range became isolated from other mountain ranges by the newly-formed desert. This desert then acted as a substantial barrier to plant migration between the ranges of southern Nevada. Irrespective of the origin of this new asexual clone of *Antennaria,* i.e., *A. soliceps,* it was now left geographically isolated.

With the warming and drying which took place, *A. aromatica*'s range would also have decreased and again become restricted to Wyoming and Montana. Even though suitable habitat of proper elevation and characteristic limestone talus does exist in southern Wyoming and in Colorado, just south of *A. aromatica*'s current range, the species is not found growing here (Bayer 1989b).

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A NEW VARIETAL DESIGNATION IN *SILENE DOUGLASII*

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Abstract

Silene douglasii var. **rupinae** ("of a rocky chasm") is described as a new variety, based on fieldwork in Washington, Oregon, and California and herbarium study of specimens throughout the range of *Silene douglasii* Hook. Plants of var. *rupinae* are endemic to rocky cliffs and promontories in the Columbia River Gorge region of Oregon and Washington. They differ from other varieties by their markedly linear leaves, with length : width ratios typically exceeding 15:1, by their sometimes glandular calyces and stems, and by petal limbs that average 1–2 mm shorter and narrower than in vars. *douglasii* and *oraria*. Corolla appendages are also shorter than in var. *oraria*. Var. *rupinae* encompasses a portion of the former var. *monantha* (Wats.) Robins. located in the Columbia River Gorge but does not include its *douglasii*-like type or those plants found in the Sierra Nevada, both of which we place in synonymy with var. *douglasii*.

Recognized since 1830 when Hooker described it from the collections of explorer David Douglas, *Silene douglasii* Hooker has historically included a number of varieties; at least eight were once accorded specific status. In their most recent revision of North American *Silene,* Hitchcock and Maguire (1947) reduced *S. douglasii* to four varieties, helping to clarify often confusing and overlapping descriptions of the taxa. Hitchcock et al. (1964) later placed one of these taxa, var. *villosa,* in synonymy with var. *douglasii,* thereby retaining this latter widespread variety and two narrowly restricted varieties, var. *oraria* and var. *monantha.*

Kruckeberg (1954, 1955, 1960, 1961, 1962, 1964) studied *Silene* cytotaxonomically and performed extensive experimental hybridizations. His artificial crosses within *S. douglasii* yielded fertile offspring, supporting the treatment of morphotypes as infraspecific categories. Yet, in spite of this work and earlier revisionary and floristic studies, taxonomic problems remain (Hitchcock and Maguire 1947; Showers 1987). In our attempt to resolve some of the difficulties in *S. douglasii* with additional biosystematic and ecological investigations, we discovered the nomenclatural complications reported here.

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[1] Authors' names are presented alphabetically.

VARIETAL RELATIONSHIPS AND TAXONOMIC HISTORY

Douglas described *Silene douglasii* as "abundant in mountain vallies, above the Grand Rapids of the Columbia, and among the Rocky Mountains, on their western declivity." Thus, it is not surprising that both Robinson (1893) and later, Hitchcock and Maguire (1947), created infraspecific names as a means of organizing the diversity they observed over this wide geographic range. In our field studies at type localities and sites of earlier collections, however, we found that some of the published morphological and geographical descriptions of the taxa did not reflect our observations. Furthermore, in the course of examining all the known types for taxa associated with *S. douglasii,* we discovered errors and inconsistencies between the designated types of the varieties and their published descriptions.

We identify two principal nomenclatural problems; one centers on the delineation of the types for var. *monantha* (Wats.) Robins. and for *S. douglasii* Hook. A second concern arises from the geographic circumscription and morphological description of var. *monantha* by different investigators.

Delineation of type for var. douglasii. Hooker based his description of *S. douglasii* on material collected by Douglas, but failed to clearly label a holotype from among three sheets now located at Kew. Unfortunately, the most likely candidate, and indeed the only Douglas sheet originally from Hooker's herbarium, is a mixed collection bearing two separate Douglas labels dated from 1825 and 1826 (Fig. 1). These separate collections on one herbarium sheet represent specimens that, in numerous descriptions written both before and after Hitchcock and Maguire's (1947) revision, correspond morphologically to at least two different varieties. Furthermore, we find no evidence that Hitchcock and Maguire examined any of these specimens at the time of their 1947 revision of the genus *Silene* (presumably the three Kew specimens were unavailable during World War II), so this problem has remained. Thus, we have now designated one of the *douglasii*-like stems on this herbarium sheet as the *douglasii* lectotype for *S. douglasii,* which thereby serves also as the type for var. *douglasii.* The specimen selected is more complete than the other possible choices and its label description ("common in the mountain vallies between Spokane and Kettle Falls and in the vallies of the Rocky Mountains near the source of the Columbia") accurately describes the broad distribution of this taxon. Moreover, the remaining *douglasii*-like specimens on this sheet are of ambiguous origin since some bear handwritten notations by Nuttall and, in fact, may represent his, rather than Douglas' collections.
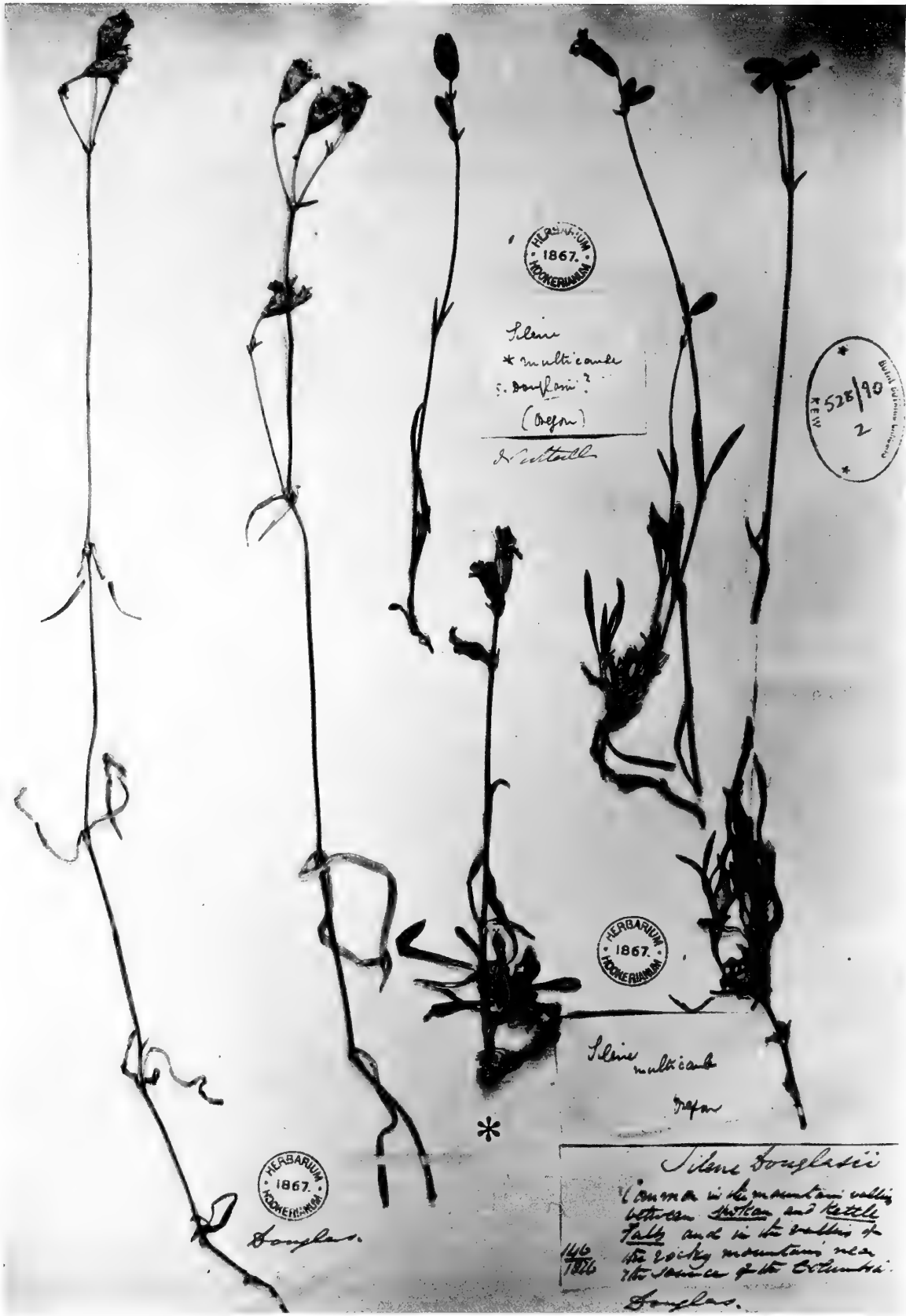
Fig. 1. Kew herbarium sheet. Asterisk at base of stem in photo denotes newly designated lectotype of *S. douglasii* var. *douglasii*, selected from the four *douglasii* stems at right. The two leftmost stems are now paratypes of var. *rupinae*.

Delineation of type, description, and range of var. monantha. Another problem arose when we inspected the Kellogg and Harford (GH) type for var. *monantha* (=*S. monantha* Watson) collected from Castle Rock, Washington and when we compared it to descriptions of this taxon by Watson (1875), Robinson (1893), Howell (1897), and Hitchcock and Maguire (1947). Specifically, we found that the morphology and geography of plants designated as var. *monantha* were similar to var. *douglasii.* For example, key characters in Watson's original description were weak, elongated stems, glabrous vestiture, and inflated calyces. Yet inflated calyces and presence of stems of varying stature are also typical of var. *douglasii* (Hitchcock and Maguire 1947). In addition, close inspection of the holotype for var. *monantha* revealed that it is not strictly glabrous, as Watson had indicated, and that is virtually inseparable from var. *douglasii* collections throughout the Northwest.

Later, Robinson (1893) treated *S. monantha* as a variety of *S. douglasii,* retaining the features noted by Watson, adding a description of the leaves as "grass-like," and extending the geographic range of var. *monantha* to include populations from California and Utah. He also described a new variety *brachycalyx* whose leaves were narrowly-oblanceolate, but puberulent (and non-viscid). The holotype is a Howell specimen from an unspecified locality in Multnomah County, Oregon, a region that includes part of the Columbia River Gorge. Four years later, Howell (1897) himself elevated var. *brachycalyx* to *S. columbiana,* describing it as smooth *or* puberulent and growing on "cliffs and rocky banks along the lower Columbia and Willamette Rivers." Thus, by this time, the epithets *monantha, brachycalyx,* and *columbiana* had been variously applied by Watson, Robinson, and Howell to populations of plants that remained indistinct in their morphology and geography.

Even Hitchcock and Maguire (1947) found it difficult to characterize the variability within *S. douglasii.* They gave little credence to either Robinson's var. *brachycalyx* or Howell's *S. columbiana,* placing both of these taxa in synonymy partly with var. *douglasii* and partly with var. *monantha.* In their monograph, they now delineated the once glabrous var. *monantha* from var. *douglasii* by its sparse, short hairs that are sometimes glandular. They further recognized var. *monantha* as a disjunct taxon with populations in the lower Columbia River Gorge near Mt. Hood and in the Sierra Nevada in California. Yet Hitchcock and Maguire (1947) still disagreed as to whether the nearly glabrous, broader-leaved plants from the Sierra Nevada (often designated as an unpublished name var. *glabrata* on herbarium sheets) might constitute yet another variety distinct from the narrow-leaved, sometimes glandular material found near the Columbia River Gorge.

Furthermore, var. *monantha* is apparently extinct in its type locality, with no known isotypes available for comparison. Although Hitchcock and Maguire (1947) had implied that there existed some glandular specimens from the type locality, most of the specimens they cite are from the Columbia River Gorge. Yet Castle Rock, Washington, the type locality of var. *monantha,* lies outside this region. Thus, the collections they cite are clearly not isotypes, and we have been unable to locate either valid isotypes or extant plants from Castle Rock. Even Howell (1897) noted that plants bearing the epithet *monantha* had not been located in the type locality subsequent to Watson's original description in 1875.

Finally, in summary, the epithet *monantha,* based on the Kellogg and Harford type, has been used for at least two different morphotypes from three separate localities. It has been inconsistently applied to sparsely pubescent (mostly eglandular), broad-leaved, *douglasii*-like material in Washington, Utah, and the Sierra Nevada and to narrow-leaved, pubescent, glandular or eglandular plants collected in the Columbia River Gorge. The epithet *brachycalyx* (=*S. columbiana*) has been variously applied to glabrous or puberulent plants that are *not* viscid. Thus, neither *monantha* nor the epithet *brachycalyx* adequately delimits any entity that is consistently distinct from var. *douglasii.*

New Varietal Designations

Based on our fieldwork throughout California, Oregon, and Washington, on studies of herbarium specimens throughout the range of *S. douglasii,* including our examination of all types (CSPU, DAV, GH, K, OSC, ORE, UC, WILLU, AND WTU), and on recent biosystematic studies (in progress), we propose retention of both vars. *douglasii* and *oraria* as distinct taxa. As indicated in the key below, var. *oraria* differs from other named varieties of *S. douglasii* by its shorter stature, broader and thicker leaves, more inflated calyces and larger flowers. We further designate as var. *rupinae* ("of a rocky chasm") those populations of narrow-leaved, glandular or eglandular plants (Fig. 2) restricted to rocky sites in the Columbia River Gorge region of Washington and Oregon. Because plants of var. *rupinae* are most readily distinguished from other named varieties by their vegetative features (i.e., discriminant functions correctly classified 95% of the individuals based on vegetative characters and only 56% based on reproductive traits) and because intervarietal crosses within *S. douglasii* yield fertile offspring (Kruckeberg 1961), we believe the rank of variety is appropriate.

A new varietal name was chosen because no previously published epithet corresponds to this entity in both geographic location and
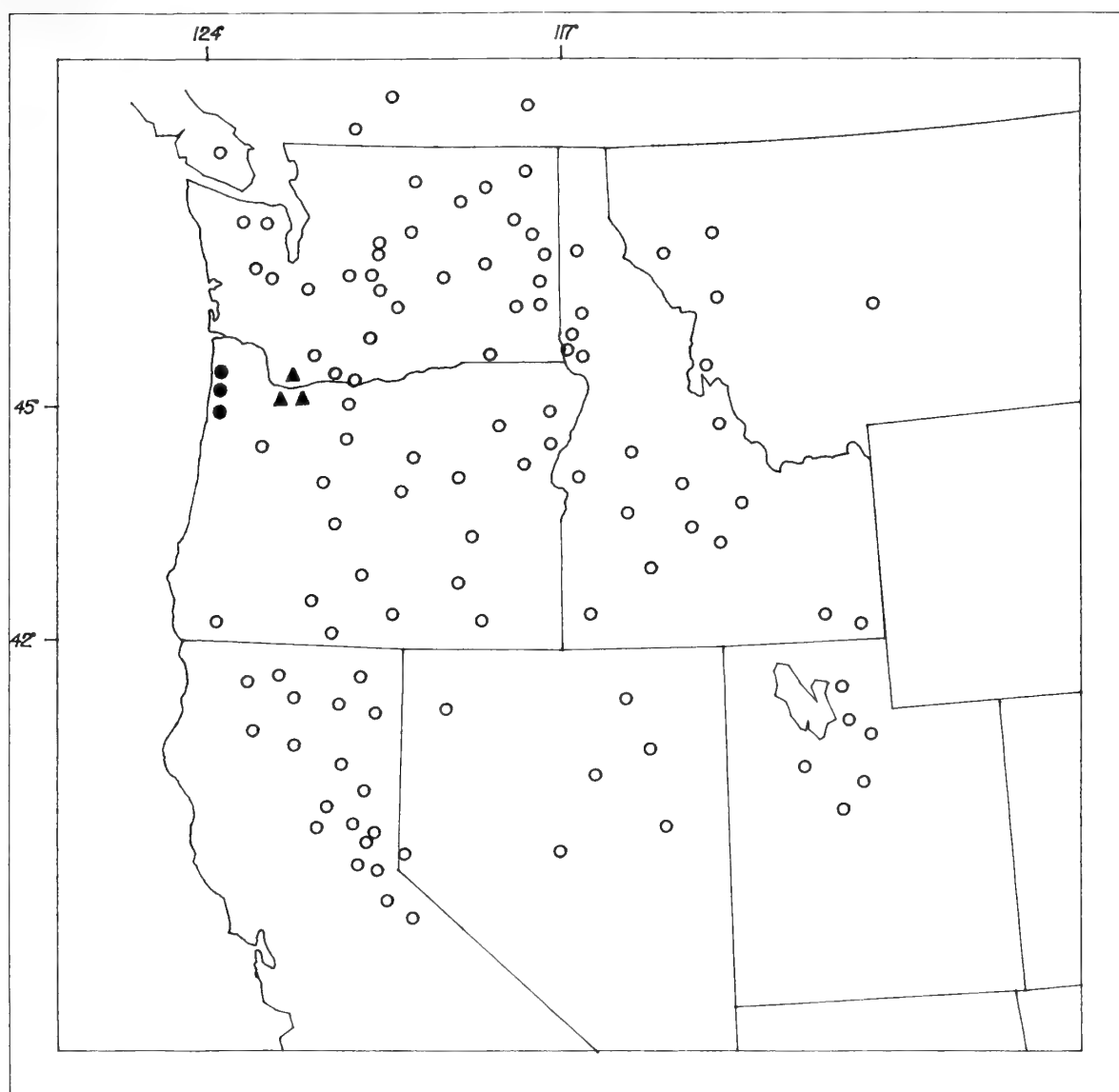
FIG. 2. Map showing distribution of varieties of *S. douglasii*. Triangles denote var. *rupinae*, closed circles var. *oraria*, and open circles var. *douglasii*.

morphology. In var. *rupinae*, we include that part of the prior-named var. *monantha* that was restricted to the Columbia River Gorge and its vicinity. We place in synonymy with var. *douglasii* that part of var. *monantha* located outside of this region because these specimens, including the Kellogg and Harford holotype and the California collections, are indistinguishable from those of var. *douglasii*. We also reject *S. douglasii* var. *brachycalyx* (=*S. columbiana*) as a name for the new variety because its lectotype is morphologically *douglasii*-like and of uncertain locality. We place other taxa previously proposed at the varietal level in synonymy with var. *douglasii* or *S. parryi* in agreement with Hitchcock and Maguire (1947). We concur with Hitchcock et al. (1964) who treat var. *villosa* Hitchc. & Mag. as synonymous with var. *douglasii*.

Key to the Varieties of *Silene douglasii*[2]

a. Plants coastal in Oregon; leaves[3] broad, 3–13 mm wide, 0.3–0.7 mm thick; flowers typically large, calyx strongly inflated, (4)7–10(12) mm in diameter at anthesis, petal limb 5–11 mm wide, often with a lateral tooth on margin. . . . .
. . . . var. *oraria* (Peck) Hitch. & Maguire
a'. Plants distributed throughout coastal and interior mountainous regions of western North America or restricted to the Columbia River Gorge in both Oregon and Washington; leaves variable in width 1.5–9 mm, not so thickened (0.1–0.5 mm); calyx narrower (3)5–8(10) mm in diameter, petal limb narrower, 1–5 mm wide, often not toothed.
  b. Cauline leaves narrow, 1.5–5.0 mm wide, typically over 15× longer than wide, often markedly linear; stem and calyx vestiture glandular or eglandular; plants distributed in rocky sites with shallow soils, in crevices and on cliff ledges along the Columbia River Gorge in Oregon and Washington. . . . .
  . . . . var. *rupinae*, var. nov.
  b'. Cauline leaves variable in width, 2–9 mm wide, and typically no more than 5–10× longer than wide; stem and calyx vestiture eglandular; plants distributed in dry sagebrush plains, open woods, and in mountainous regions from the Rocky Mountains westward to the Coast Ranges of British Columbia, Washington, and Oregon, south to central (Alpine County, California). . . . .
  . . . . var. *douglasii*

Silene douglasii var. **rupinae** Kephart and Sturgeon, var. nov.— TYPES: USA, Oregon, Multnomah County, Angel's Rest, elevation 1600', rocky promontory and slopes above the Columbia River Gorge, with *Lomatium, Allium, Eriophyllum,* and *Cerastium,* June 28, 1988. Kephart and Sturgeon #125 (holotype, OSC; isotypes, DAV, GH, K, ORE, OSC, CSPU, UC, WILLU, WTU).

A varietatibus ceteris foliis linearioribus 2–3 mm latis plerumque plus quam 40 mm longis, caulibus et calycibus interdum glandulosis differt; flores ad var. *douglasii* similares sed limbo petalorum circa 1 mm breviore angustioreque; flores a var. *oraria* limbo petalorum circa 2 mm breviore angustioreque, appendicibus 1.5 mm brevioribus differant.

Perennial herb (13)25–30(47) cm tall; multiple stems arising near base of plant above a deep taproot; pubescence simple, glandular or eglandular varying within and among populations; leaves linearoblanceolate; cauline leaves (14)35–75(84) mm long to (1.5)2–3(5) mm wide (length : width ratio approximately 20:1), 0.1–0.4 mm thick; margins entire, tips acute tapering gradually to petiole-like bases; inflorescence cymose with 1–3(6) flowers; pedicels of central flowers

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[2] Measurements are mid-ranges for fresh material collected identically from 131 plants representing a total of seven sites and ≥2 populations per variety.
[3] Standardized to third node beneath open center flower of cyme. Most measurements rounded to nearest whole integer for endpoints of range.

(3)15–30(59) mm long; calyces inflated, glandular or eglandular, (8)11–14(15) mm long, (4)6–7(10) mm wide, lobes (2)2.5–3(4) mm long; corolla white, often red-tinged beneath; petal claw (9)11–16(17) mm long, exerted beyond calyx; petal limb (2)4.0–7(8) mm long, (1)2.5–4.5(5) mm wide, bilobed, incised to (1)1.5–2.5(3) mm; appendages variable, (0.5)1–3(4) mm long, (0.5)1–2 (3)mm wide; styles (2)3; carpophore at base of ovary (1)2.5–4(5) mm long surrounded by nectaries and becoming stipitate in fruit; fruit a capsule; seeds many with papillate margins.

Found in rocky places on both sides of the Columbia River Gorge in Oregon and Washington; centered in the region between Portland and The Dalles; common in the vicinity of Bridal Veil Falls, Oneonta Gorge, and Cape Horn.

PARATYPES: Douglas [two sheets, one mixed collection from 1825 and 1826, second has no date] (K), Howell 575 [6-1886] (GH), Howell [no number, 7-12-1881] (ORE), Suksdorf [6-28-1882] (GH), Suksdorf 2436 [8-18-1894] (GH), Suksdorf 10526 [1920–22] (WTU, GH).

DISCUSSION

Hitchcock and Maguire (1947) called attention to much morphological variability in North American *Silene.* Such diversity is to be expected in geographically widespread species, and particularly where, as in *S. douglasii,* populations are isolated from one another on mountain-tops, along coastal headlands, and in rocky gorges in otherwise forested areas. More surprising, perhaps, is the degree of polymorphism we observed within many populations of this species (Fig. 3) (Kephart and Sturgeon unpublished). One population in the Columbia River Gorge, for example, exhibits polymorphism for glandularity of calyx and stem pubescence; also a single plant at the same locality shows leaf and floral characters that could imply placement in var. *oraria* were it not for the overwhelming preponderance of narrow-leaved plants at that locality. Similarly, at Cascade Head, the type locality for var. *oraria,* occasional plants are found that, in the absence of the geographical and population context, could be assigned morphologically to varieties *rupinae* or *douglasii* (Kephart 1986).

Many of the past difficulties in delineating infraspecific taxa in *S. douglasii* stem from this high level of polymorphism (similar difficulties also characterize Western American *Silene* generally). For example, Hitchcock and Maguire (1947) used density and length of trichomes, glandularity, and the presence or absence of pubescence to distinguish among varieties within *S. douglasii,* using them in their key. Yet within a single variety, *monantha,* they included specimens which were glabrous or pubescent, and glandular or eglan-

FIG. 3. Variation in leaf morphology within *S. douglasii* var. *douglasii* at a single locality.

dular. Similarly, one of several characters that differentiates *S. douglasii* from *S. parryi* is the copious glandularity of the latter taxon, yet glandular hairs occur within both species. In fact, two varieties, *viscida* and *macounii,* formerly ascribed to *S. douglasii,* were later transferred to *S. parryi* (Hitchcock and Maguire 1947). Floral characters, including the number of petal lobes, and style number, also vary within and among species of *Silene* (e.g., *S. parryi* was first described as a species of *Lychnis,* based on style number, until it was recognized that this character varied within the genus *Silene*).

Thus, considerable population and geographic variation in the frequency of various morphotypes occurs within *Silene* and *S. douglasii* (e.g., as noted above, narrow-leaved forms, which occur in high

frequency in Columbia River Gorge populations, may be found elsewhere albeit in much lower frequency). Yet recognizable taxa exist at the varietal and species levels. Therefore, in defining the appropriate taxonomy, we chose to delineate var. *rupinae* both by its morphology and its geographic location; i.e., we restrict the designation var. *rupinae* to only those narrow-leaved, glandular or eglandular individuals that are found in the Columbia River Gorge region of Oregon and Washington. Two alternatives were considered: (1) recognizing a single, polymorphic species without varietal distinctions, and (2) treating the varietal groups as species. The latter alternative is untenable because no apparent barriers to interbreeding exist among taxa (Kruckeberg 1961). The former obscures the clear geographic differences in frequency of multiple characters; in addition, Kephart and Sturgeon (1989) found these characters to correctly predict varietal groups (*douglasii, oraria,* and *rupinae*) for 94% of the individuals classified.

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SYSTEMATICS OF *MALACOTHRIX PHAEOCARPA,* A NEW SPECIES RELATED TO *M. FLOCCIFERA* (ASTERACEAE: LACTUCEAE)

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ABSTRACT

Malacothrix phaeocarpa, new species from the California Floristic Province, is described. The new species is self-compatible and self-pollinating, and closely resembles the self-incompatible species *M. floccifera* from which it differs chromosomally and in several floral features.

During a study of herbarium specimens of *Malacothrix floccifera* (DC.) S. F. Blake a number of atypical specimens were found that were very similar to *M. floccifera* in vegetative features but different in several floral features. Chromosome associations in meiosis in hybrids, produced in cultivation between representatives of three populations of these plants and representatives of four populations of *M. floccifera,* indicate that there are also chromosomal differences. In this paper a new species, *M. phaeocarpa,* will be described, and evidence concerning its relationships and origin will be discussed.

Malacothrix phaeocarpa W. Davis, sp. nov.—TYPE: USA, California, San Luis Obispo Co., north side of west Cuesta Ridge, along unpaved road, ca. 0.3 mi S of intersection with Tassajera Creek Rd, 1.8 mi W of U.S. 101, SE-facing slopes, in loose shale at edge of roadcut, 17 May 1990, *Davis 462* (holotype, DS; isotypes, CAS, DHL, MO, OBI, RSA, SBBG, UC, US). Careful examination of the holotypes of *Malacothrix obtusa* Bentham (K), and *M. parvifolia* Bentham (K) indicates that both are *M. floccifera,* not *M. phaeocarpa,* and that Blake (1924) was correct when he reduced *M. obtusa* to *M. floccifera.*

Herbae annuae, 5–44 cm altae e radice palari orientes. Caules superi vel e base ramosi, subglauci, subrecti. Folia basales rosulata, oblanceolata vel obovata, subcarnosa, 2–7 cm longa, 6–20 mm lata, marginibus 3–8 paribus dentium et lobis curtis, latis subaequalibus, plerumque dentatis, acuti-vel obtuso-apiculatis et basi lobi omnis areis pilorum curtorum alborum praedita. Folia caulina infima foliis basilibus similia, sursum multum reducta, lanceolata, ovata vel oblanceolata. Folia suprema lobis basalibus, curtis, angustatis, in paribus 1–2 praedita, in ⅔ areae distalis margines integros praebentia.

Capitula per anthesin 2–3.6 mm diametro, basi rotunda. Involucrum 5–8 mm, phyllariis externis plerumque viridibus, deltoideis vel lanceolatis, marginibus albis et phyllariis interioribus linearibus vel lanceolatis, acuti-apiculatis praedita. Receptaculum nudum. Flores 30–65, corollis 5.4–8.0 mm, albis et ligulis plerumque exsertis 1.5–2.5 mm praediti. Fructus 1.2–2.0 mm, brunnei vel rubro-brunnei, costis 15, distinctis acuti-apiculatis earum 5 prominentibus et pappo externo coronam scariam crenatam setis persistentibus carentem formanti praediti. $2n=14$. Auto–gonimae.

Annual, 5–44 cm from a taproot. Stems branched above or from the base, somewhat glaucous, generally erect. Basal leaves in a rosette, oblanceolate to obovate, somewhat fleshy, 2–7 cm long, 6–20 mm wide, margins with 3–8 pairs of teeth and short, broad, nearly equal, generally toothed lobes 2–7 mm with acute or blunt apices, patches of short, white hair generally at the base of each lobe. Lowest cauline leaves similar to basal leaves, greatly reduced upward, lanceolate, ovate, or oblanceolate. Uppermost leaves with 1–2 pairs of short, narrow basal lobes, the distal ⅔ with entire margins. Heads 2–3.6 mm in diameter in flower, base rounded. Involucre 5–8 mm; outer phyllaries generally green, deltoid to lanceolate, margins white; inner phyllaries linear to lanceolate, with acute apices. Receptacle without bristles. Flowers 30–65; corolla 5.5–8.0 mm, white; outer ligules generally exserted 1.5–2.5 mm; fruit 1.2–2 mm, medium brown or reddish-brown, with 15 well defined ribs with acute apices, 5 prominent; outer pappus a scarious, crenate crown with no persistent bristles. $2n=14$. Self-compatible and self-pollinating.

PARATYPES. USA, California, Monterey Co., near stage road to Jolon, *Dudley s.n.* (DS 889, not DS 890); along the trail to Skinners Ridge above Boucher's Gap, *Howitt 1146* (CAS); gravelly hills, Monterey, *Parry s.n.*, Mexican Boundary Survey (K, NY); Monterey, *Torrey s.n.* (K); San Luis Obispo Co., cleared chaparral, Santa Barbara Rd, Atascadero, Santa Lucia Mts., *Hardham 4810* (CAS, SBBG, UCSB); on sandstone in burned chaparral area, Franklin Cr, Adelaida, Santa Lucia Mts., *Hardham 6915* (UCSB); burn in *Pinus attenuata* woods E of Cuesta Grade, *Hardham 9012* (UCSB); ridge SE of Cuesta Pass, disintegrating shale, *Hoover 8916* (CAS, OBI); Cuesta Ridge Botanical Area, extreme N edge along powerline road, 0.3 mi SW of intersection with Tassajera Creek Road, *Junak 4122* (DHL, SBBG); Cuesta Ridge Botanical Area, along private dirt road, ca. 1.8 mi W of Hwy 101, and 0.3 mi S of Tassajera Creek Road, *Junak 4350* (SBBG); Santa Barbara Co., near Santa Barbara, Santa Inez Mts., *T.S. Brandegee s.n.*, (UC); near summit of Harris Grade, Purisima Ridge, *Breedlove 2596* (DS, UCSB); dry slope in pine woodland, road from Figueroa Mt. to Cachuma Saddle, just N of Ranger Peak, *Chandler 3109* (SBBG); along Hwy 1, 3.2 mi S of

junction with hwy 135, above oil pumping station in grove of Bishop pine on diatomaceous soil, *Davis 455,* (DHL, SBBG); Painted Cave Ranch, *Eastwood 116* (US); gravelly slopes, Figueroa Mt., San Rafael Mts., *Hoffman s.n.* (SBBG); open gravelly flat, Figueroa Mt., *Hoffman s.n.* (SBBG); brushy slope, 5 mi N of Lompoc, *Hoffman s.n.* (SBBG); Purisima Hills, *Jepson 11957* (JEPS); Camino Cielo, between San Marcos Pass and Bush Peak, area of Refugio Pass burn of 1955, *Pollard s.n.* (CAS); on burn among Bishop pine on N side of Harris Grade, Purisima Hills, *Smith 6290* (DHL, SBBG); chaparral burn on El Camino Cielo, ca. 5.4 mi W of San Marcos Pass, *Smith 4585* (SBBG); hillside, chaparral burn along El Camino Cielo, ca. 6.2 mi W of San Marcos Pass, approximately S of Hot Springs Cyn, *Smith 4529* (SBBG); Santa Clara Co., ranch below Cattermoles, Santa Cruz Mts., Loma Prieta, *Dudley s.n.* (DS).

Malacothrix floccifera and *M. phaeocarpa* are endemic to the California Floristic Province as described by Raven and Axelrod (1978). Although *M. floccifera* is relatively widely distributed, *M. phaeocarpa* apparently is restricted to the southwestern margins of the range of *M. floccifera* (Fig. 1), and generally falls within the distribution of *M. floccifera*; however, *M. phaeocarpa* occurs in the Purisima Hills, Santa Barbara County, where *M. floccifera* apparently has not been collected. Although *M. floccifera* and *M. phaeocarpa* generally occupy similar habitats (loose soils on burns or slides) in the southern portion of the distribution of the former, no sympatric populations are known. However, *M. phaeocarpa* has been collected in chaparral within three miles of a population of *M. floccifera* in Santa Barbara County.

Found at elevations from 100–1400 m, *Malacothrix phaeocarpa* grows in openings in chaparral, but also occurs in openings in *Pinus attenuata* or *Pinus muricata* woods. The species occurs on soils derived from shale, sandstone or diatomaceous earth. Associated species in San Luis Obispo and Ventura counties include *Adenostoma fasciculatum, Arctostaphylos gladulosa* ssp. *gladulosa, Calandrinia breweri, Cryptantha clevelandii, Dendromecon rigida, Emmenanthe penduliflora, Eriogonum cithariforme, Erodium cicutarium, Eschscholzia caespitosa, Hypochoeris glabra, Lactuca serriola, Lotus junceus, Lotus salsuginosus, Pinus attenuata, Pinus muricata, Pseudotsuga menziesii, Quercus durata, Quercus wislizenii, Senecio vulgaris,* and *Silene multinervia.*

Populations of *M. floccifera* are associated with a number of plant communities including chaparral, juniper-digger pine woods, oak woodlands, redwood forests, transition forests, and yellow pine forests. The species grows on serpentine soils, loose clay soils, gravelly soils, or fine sand at elevations from 100–2100 m. Associated species in San Luis Obispo and Santa Barbara counties include *Adenostoma fasciculatum, Artemesia tridentata, Calystegia fulcrata* ssp. *mala-*
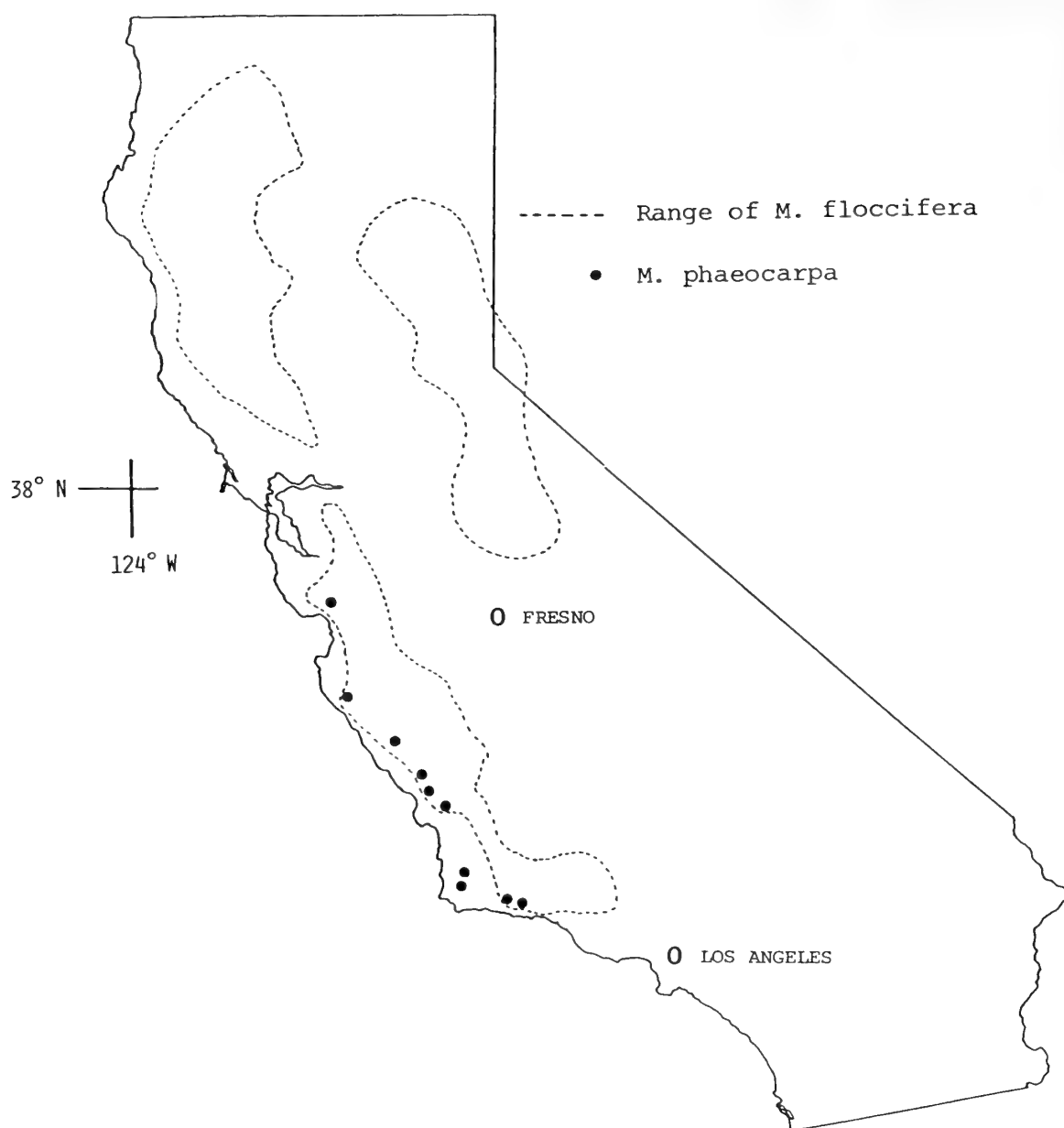
Fig. 1. Distribution of *Malacothrix floccifera*, and populations of *M. phaeocarpa* in California.

cophylla, Dendromecon ridiga, Emmenanthe penduliflora, Eriogonum fasciculatum, Galium andrewsii, Langloisia schottii, Lotus salsuginosus, Phacelia cicutaria, Quercus douglasii, Rhus trilobata, and *Salvia columbariae.* In the western portion of its distribution, *M. floccifera* parallels the distribution of chaparral in the California Floristic Province in the Transverse Ranges in Ventura County, and northward in the Coast Ranges. In the eastern portion of its distribution *M. floccifera* follows the distribution of chaparral in the Sierra Nevada north of Madera County (Fig. 1), but is associated with other plant communities at higher elevation.

On the basis of growth habit, leaf morphology, leaf hair distribution, involucre length, involucre morphology, and fruit size *Malacothrix phaeocarpa* and *M. floccifera* are not consistently distin-

TABLE 1. A COMPARISON OF *MALACOTHRIX FLOCCIFERA* AND *M. PHAEOCARPA* GROWING TOGETHER IN A GROWTH CHAMBER.

	M. floccifera	M. phaeocarpa
Involucre height (mm)	4.2–9.0	5.1–8.0
Number of involucral bracts	16–30	15–19
Width of flower heads in flower (mm)	2.7–4.2	2.2–4.5
Number of florets in a head	19–63	21–66
Corolla length (mm)	7.2–15.1	5.4–8.0
Ligule length (mm)	5.0–10.0	2.1–4.2
Ligule width (mm)	2.7–4.2	1.0–1.7
Outer ligule exsertion (mm)	5.4–9.0	1.5–2.5
Length of receptacle bristles (mm)	2.3–3.0	none
Stamen length (mm)	5.5–7.0	3.5–5.4
Distance, tip of anther to base of style branches (mm)	1.2–4.1	0.2–1.5
Achene length (mm)	1.3–2.1	1.4–2.0
Length of inner pappus (mm)	3.2–5.8	3.6–4.3
Growth rate after bolting (mm/day)	1.5–3.2	3.4–4.6

guishable (Table 1). The two species differ, however, in several floral features. In *M. floccifera* ligules are well-exserted beyond the involucre; the receptacle has thin, smooth, somewhat fragile bristles as long as 4 mm; there is no outer pappus on achenes; and, apices of intermediate achene ribs between pairs of strong ribs are flattened. In *M. phaeocarpa* ligules extend less than 3 mm beyond the involucre; the receptacle is without bristles; a scarious, crenate outer pappus is present at the achene apex; and, the intermediate ribs of the achene are well-defined. Ligules of *M. phaeocarpa* are white to cream-white, and bear an abaxial purplish stripe. Ligules of *M. floccifera* are generally white with an abaxial purplish stripe, but populations of yellow-flowered plants occur in the western area of distribution, and are indistinguishable from white-flowered plants in features other than flower color. In several populations of *M. floccifera* along the road through Rose Valley, Ventura County, there is found a continuum of corolla color shades ranging from white to yellow.

Achenes of *Malacothrix phaeocarpa* are dichromic. In progenies in growth chamber culture 17% of the achenes were reddish-brown, and were found in the distal rows of mature flower heads. The rest of the achenes were light to medium brown, and generally were found in the inner portion of the flower head. Achenes of *M. floccifera* are grey, brown, or purple-brown; in a majority of them a dark line is visible through the fruit coat in the middle portion of the achene. The source of the line is a narrow ring of black pigment circling the embryo just below the base of the coteledons. In cross-section, the interior tissue of the embryo is white; the black pigment occurs only in the outer cells.

RESULTS OF GROWTH CHAMBER STUDIES

Representatives of two populations of *M. phaeocarpa* in Santa Barbara County (Breedlove 2596, SBBG; Davis 445, DHL, SBBG) and one population in San Luis Obispo County (Junak 4122, SBBG, DHL) were grown in growth chambers at the University of Louisville (see Davis and Philbrick 1986 for a description of general methods). Propagated at the same time were representatives of four populations of *M. floccifera,* two in Placer County (Baad 4757, MCAF; Baad 3403, MCAF) and two in Ventura County (Davis 401, DHL; Junak 3046, DHL, SBBG). Less than 10% of the achenes of either species germinated in petri dishes; achene tips were punctured with a needle to increase germination rate. In general, plants of *M. phaeocarpa* bolted, flowered, and commenced senescence sooner than plants of *M. floccifera* growing alongside them. In addition, heads of *M. phaeocarpa* were noticeably less nodding in bud than heads of *M. floccifera.* Meiotic chromosome counts of $2n=7_{II}$, and root tip mitotic counts of $2n=14$ were obtained for both species; pollen stainability in plants grown from wild achenes was 90–100%.

All *M. floccifera* grown from wild achenes (30 plants), and from intra-populational crosses (34 plants), was self-incompatible. However, eight of 15 plants from intraspecific crosses between representatives of a Placer County population and representatives of a Ventura County population were self-compatible; none of these plants had any of the morphological diagnostic features of *M. phaeocarpa.*

All *M. phaeocarpa* grown from wild achenes (26 plants), or from achenes from self- or sister-pollinations (35 plants) was self-compatible and self-pollinating.

Artificial interspecific hybrids between *Malacothrix floccifera* and *M. phaeocarpa* were difficult to produce; only 15 filled achenes were produced from 115 cross-pollinations involving *M. floccifera* as the female parent. Eight achenes germinated and produced mature plants; 1 plant was male sterile and a product of self-fertilization via the mentor effect (Davis 1984), and seven plants were hybrids with stainable pollen of 0–10%. One hybrid was produced from crosses involving *M. phaeocarpa* as the female parent; it had 3% stainable pollen. Chromosome pairing was variable in hybrids and the maximum chromosome association was 2 pairs, six univalents, and a chain of four.

THE ORIGIN OF MALACOTHRIX PHAEOCARPA

Of all of the extant species of *Malacothrix, M. floccifera* is the one most similar to *M. phaeocarpa* in a majority of features including growth habit, details of vegetative morphology, involucre morphology, and habitat preference. Breeding system differences support

the hypothesis that the relationship between *M. floccifera* and *M. phaeocarpa* is a progenitor-derivative one. Some of the floral differences between the allogamous *M. floccifera* and the autogamous *M. phaeocarpa* are of the sort that have been found to be associated with the evolution of autogamy in other groups of plants (Wyatt 1988). These include differences in corolla length, in degree of exsertion of ligules, in ligule width, in anther length, and in distance from anther tip to base of style branches (Table 1). Other differences, however, such as presence of numerous, long receptacle bristles in *M. floccifera* (none in *M. phaeocarpa*), a well-developed outer pappus in *M. phaeocarpa* (absent in *M. floccifera*), well-defined intermediate ribs of achenes of *M. phaeocarpa* (flattened in *M. floccifera*), and differences in chromosome structure are not generally correlated with a shift in breeding system, and suggest that the origin of *M. phaeocarpa* may have involved a multistep process of selection over an extended period of time.

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FRUITING PLANT ATTRACTIVENESS TO AVIAN SEED DISPERSERS: NATIVE VS. INVASIVE *CRATAEGUS* IN WESTERN OREGON

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Abstract

Crataegus monogyna, a hawthorn native to Europe, has successfully invaded much of North America since its introduction approximately 200 years ago. Successful dispersal by avian frugivores, relative to the native biota, may be one reason why *C. monogyna* is so invasive. To address this hypothesis I compared the attractiveness of *C. monogyna* and *C. douglasii suksdorfii* (the native hawthorn) to their primary dispersal agent (American robins) in western Oregon. A companion study in western Oregon (Sallabanks 1993) identified three *Crataegus* traits correlated with pome removal by robins: pome crop size, mean pome size, and mean pome pulp-to-pyrene ratio. With respect to these dispersal-related traits, *C. monogyna* was found to be superior to its native counterpart, producing larger displays of higher quality pomes. These results offer an explanation for the observed patterns of distribution and abundance of *C. monogyna* and *C. douglasii suksdorfii* at the study site specifically, and in western Oregon in general. To conclude I suggest possible recommendations for management against *C. monogyna* and for frugivorous birds.

Some animal-dispersed plants produce fleshy fruits as a nutritional reward to frugivores in exchange for seed dissemination (Howe 1986). The attractiveness of fruiting plants to frugivores plays an essential role in dispersal success and may have important implications for plant species invasion. Frugivorous mammals have significantly accelerated the invasion of the western United States by *Carpobrotus edulis* L. (Aizoaceae) (D'Antonio 1990). Birds were found to play an important role in the invasion of mediterranean-climate zone South Africa by *Acacia cyclops* A. Cunn. ex G. Don. (Mimosoideae) (Glyphis et al. 1981). Similarly, birds dispersed the seeds of *Myrica faya* Ait. (Myricaceae), enabling this species to colonize Hawaii (LaRosa et al. 1985; Walker 1990; Woodward et al. 1990).

In the western United States, the native hawthorn, *Crataegus douglasii* Lindl. var. *suksdorfii* Sarg. (Rosaceae), is restricted in its range from British Columbia to northern California, and east through Idaho to Montana (Hitchcock et al. 1961; Brunsfield and Johnson 1990; T. A. Dickinson and R. M. Love personal communications). The invasive European hawthorn, *C. monogyna* Jacq., arrived in the United States in the early 19th century (Douglas 1914) and has

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since spread rapidly throughout much of North America, doing particularly well in the Pacific Northwest and the Great Lakes–New England regions. *Crataegus* is dispersed by producing polypyrenous pomes (fruits) to attract primarily avian frugivores (De Boer 1979; Courtney and Manzur 1985; Herrera 1987; Dickinson and Campbell 1991; Sallabanks 1992).

In this paper I focus on a study site in the Willamette Valley of western Oregon to examine differences in the dispersal potential between the native and invasive *Crataegus*. The results presented here may be applicable to other geographic regions; in Australia, for example, *C. monogyna* is expanding its range at a rate of 120 m/yr (Smith 1985) due to dispersal by birds (Mulvaney 1986; Bass 1989) and marsupials (Bass 1990). Specifically, I compare the attractiveness of both *C. monogyna* and *C. douglasii suksdorfii* (henceforth "*C. suksdorfii*") to their primary dispersal agent, the American robin, *Turdus migratorius* L. In a companion study conducted at the same study site (Sallabanks 1993), it was determined which plant traits were correlated with the foraging choices of robins. Here I compare *C. monogyna* and *C. suksdorfii* with respect to these dispersal-related traits and discuss implications for the native and invasive species. More extensive data on fruiting and frugivory in the *C. monogyna–T. migratorius* system per se are documented elsewhere (Sallabanks 1992).

Methods

Study site. Field-work was conducted on the Nature Conservancy's Cogswell-Foster Reserve in Linn County, western Oregon. *C. suksdorfii* is native to the Reserve, whereas *C. monogyna* was introduced approximately 100 years ago (Love and Feigen 1978) and now comprises approximately 70% of the *Crataegus* population (Love 1980). *C. suksdorfii* comprises only 10% of the *Crataegus* population, the remaining 20% being hybrids between the native and invasive *Crataegus* (Love 1980). At the study site, the only dispersers of *Crataegus* were robins. Cedar waxwings, *Bombycilla cedrorum* Vieillot, were occasionally observed flying overhead but rarely foraged; their role in the dispersal of *Crataegus* is therefore assumed to be negligible.

Correlates of pyrene dispersal. During the winters of 1989–1990 and 1990–1991, I monitored pome removal by robins from a large population (n > 200) of fruiting *C. monogyna* plants at the study site. Several plant traits were also measured and then regressed against pome removal to determine predictors of pyrene dispersal rates. The methods used and results obtained are described in detail elsewhere (Sallabanks 1993). I limited my analyses to *C. monogyna* because

C. suksdorfii was not present in sufficient numbers and typically experienced negligible rates of pome removal (personal observation). In addition, the determination of which traits were correlated with the foraging choices of robins involved manipulating plants by removing pomes and entire branches. This kind of treatment for the already uncommon *C. suksdorfii* was considered unjustifiable.

C. monogyna vs. C. suksdorfii. In August 1990, in order to compare traits between the native and invasive *Crataegus,* I located all fruiting *C. suksdorfii* plants (n = 44) at the study site and measured pome crop sizes by systematically counting the number of pomes on all branches. I then arbitrarily collected samples of approximately 20–50 pomes from each plant, and within 48 hours, drew 20 pomes from each sample for the following analyses. Each pome was measured in diameter and weighed to the nearest milligram. Pyrenes were then dissected from each pome, cleaned of pulp, and weighed. Knowing pome and pyrene weight, I calculated pulp weight and pulp-to-pyrene ratio. In addition, I recorded the number of pyrenes per pome. In September 1990, I located the majority of fruiting *C. monogyna* plants (n = 217) at the study site and analyzed them for the same seven characters as for *C. suksdorfii.* For both *Crataegus* species, pomes were sampled on the first day that robins were observed feeding on them (*C. suksdorfii,* 18 August 1990; *C. monogyna,* 22 September 1990).

RESULTS

Correlates of pyrene dispersal. The results presented here appear in more detail elsewhere (Sallabanks 1993); here I provide only what is relevant to the ensuing discussion. Three traits were found to be significantly and positively correlated with rates of pome removal from *C. monogyna* plants by robins at the study site: pome crop size, mean pome size, and mean pome pulp-to-pyrene ratio. Although pyrene dispersal per se was not measured, pome removal is a correlate of dispersal success; plants with larger pome crops, larger pomes, and pomes with higher pulp-to-pyrene ratios therefore had potentially higher rates of dispersal.

C. monogyna vs. C. suksdorfii. Six of the seven traits measured were significantly greater for *C. monogyna* compared with *C. suksdorfii* (Mann-Whitney U-tests; Table 1). Only the number of pyrenes per pome was significantly lower for *C. monogyna.* These results were typical of other years (personal observation; R. M. Love unpublished data).

TABLE 1. COMPARISON BETWEEN *C. MONOGYNA* AND *C. SUKSDORFII* FOR THE SEVEN TRAITS MEASURED. Values are means ± SE.

	C. monogyna	*C. suksdorfii*	Mann-Whitney U-test	
	(N = 217)	(N = 44)	U	P
Pome crop size				
(pomes per plant)	2721 ± 301	1072 ± 203	3545.5	<0.025
Pome diameter (mm)	9.05 ± 0.06	7.89 ± 0.09	1114.0	<0.001
Pome weight (mg)	485.38 ± 7.20	276.13 ± 7.18	135.0	<0.001
Pulp weight (mg)	372.68 ± 6.48	191.06 ± 5.76	148.0	<0.001
Pyrene weight (mg)	112.76 ± 1.66	85.08 ± 2.85	1650.5	<0.001
Pulp-to-pyrene ratio	3.44 ± 0.06	2.39 ± 0.09	1446.0	<0.001
Number pyrenes per pome	1.02 ± 0.01	4.68 ± 0.05	0	<0.001

DISCUSSION

Attractiveness to dispersers: C. monogyna vs. C. suksdorfii. Fruiting plants with larger fruit displays can achieve greater dispersal success for two reasons. Firstly, plants with large fruit displays are more conspicuous and are therefore more likely to be visited by frugivores (Snow 1971; Howe and Estabrook 1977). Secondly, frugivores may prefer to stay in plants with large fruit displays once they've found them because less time is wasted in search and travel; foraging is therefore more efficient (Martin 1985). *C. monogyna* bushes at the study site with larger pome displays were more likely to be visited by robins (Sallabanks 1992) and had a greater proportion of their pome crops removed (Sallabanks 1993). Differences in pome crop size between *C. monogyna* and *C. suksdorfii* (Table 1) may therefore lead to differences in robin visitation rates and fruit removal rates, and ultimately, pyrene dispersal rates. Similar results are reported by Knight (1986): alien fruiting species that are successful invaders of the south-western Cape of southern Africa, in general, have larger and more conspicuous fruit displays than many indigenous species.

Robins also consume a higher proportion of the pome crop from *C. monogyna* plants with larger pomes (Sallabanks 1993). Larger pomes contain more pulp compared with smaller pomes in both *Crataegus* species (Sallabanks 1992; unpublished data) and are therefore more nutritionally rewarding. Because *C. monogyna* pomes are larger than *C. suksdorfii* pomes (Table 1), they may therefore be preferred by robins. Furthermore, the pyrenes of *C. monogyna* are both larger and occur singly compared with those of *C. suksdorfii* (Table 1). Regurgitation of pyrenes or separation of pyrenes from pulp in the gut is therefore likely to be accomplished more efficiently for *C. monogyna* compared with *C. suksdorfii* (Levey and Grajal

1991; Murray et al. 1991). These factors suggest that *C. monogyna* pomes are more profitable to frugivores compared with those of *C. suksdorfii.*

Robins also prefer *C. monogyna* plants with higher mean pome pulp-to-pyrene ratios (Sallabanks 1993). The ratio of pulp-to-pyrene is a good approximation of pome profitability because it represents both the benefit in digestible pulp and cost in indigestible pyrene that a frugivore must consume (Howe 1986). From an energetic viewpoint, *C. monogyna* pomes are nearer the dispersers' optimum (high food : ballast ratio), whereas *C. suksdorfii* pomes are nearer the plants' optimum (low food : ballast ratio) (Herrera 1981). With respect to pulp-to-pyrene ratio, therefore, *C. monogyna* pomes are more attractive to dispersers compared with those of *C. suksdorfii* (Table 1).

C. monogyna and *C. suksdorfii* also differ in the color of ripe pomes; ripe pomes of *C. monogyna* are red, whereas those of *C. suksdorfii* are black. Although red pomes may be more conspicuous than black pomes, these color differences may not affect rates of pyrene dispersal. Most "bird-fruits" are red and/or black (Willson and Whelan 1990) and choice-tests with various *Turdus* species have found no consistent preferences for either color (Brown 1974; Willson et al. 1990; Murray et al. 1991).

Because *C. suksdorfii* pomes contain more pyrenes than those of their invasive counterparts (Table 1), it may be argued that any differences in attractiveness to frugivores are compensated for by increased pyrene dispersal per pome. Unfortunately for *C. suksdorfii,* however, often only one pyrene per pome contains a true seed (Dickinson and Campbell 1991). For *Crataegus* pomes to ripen, at least one pyrene must contain a seed; all *C. monogyna* pomes eaten by robins therefore contain seeds. In short, despite large differences in apparent seed number, seed dispersal per pome is probably quite comparable between the native and invasive *Crataegus.*

Fruiting phenology. An important aspect of seed dispersal, in addition to the production of attractive fruits, is the timing of fruit ripening (Thompson and Willson 1979). Rapid removal of ripe fruits is important for some summer and fall fruiting species because of a high probability of fruit destruction by invertebrates (Thompson and Willson 1978; Sallabanks and Courtney 1992). For instance, *Pyracantha coccinea* Roemer (Rosaceae) does well as an introduced species in the Mediterranean because it offers late ripening fruits at a period when other fruits are scarce (Debussche and Isenmann 1990).

Because *C. monogyna* and *C. suksdorfii* do not ripen synchronously, it is possible that fruit and frugivore phenology explain much of the variation in relative dispersal success. If phenology was the

only factor affecting dispersal success, however, then *C. monogyna* would be invasive only where it ripened without competition from native *Crataegus* ripening at the same time. This is not the case; many native *Crataegus* species ripen their pomes for dispersal during the fall and winter months in other parts of the United States where *C. monogyna* has also successfully colonized. Stiles (1980), for example, documents nine species of native *Crataegus* ripening their pomes in September and October in the eastern deciduous forest (i.e., at the same time as *C. monogyna*). Studier et al. (1988) also report that ripe pomes of the Washington hawthorn, *C. phaenopyrum* (L.f.) Med., are eaten by birds in February and March in Michigan.

Implications for native biota. While the results presented in this paper are by no means conclusive, they nevertheless offer an explanation for the observed patterns of distribution and abundance of *C. monogyna* and *C. suksdorfii* at the study site specifically, and in western Oregon in general. It is important to point out that traits which are shown to explain differential dispersal success in an intraspecific context may not necessarily be applicable in an interspecific context. Furthermore, efficient dispersal by frugivores may not be the only reason for the success of *C. monogyna*; other differences may exist between the native and invasive species (e.g., levels of seed predation, seedling performance and response to the successional mosaic, and/or demographic patterns). Clearly, future research must test the hypothesis established here by specifically examining the actual dispersal success of *C. suksdorfii* relative to *C. monogyna.*

Factors affecting species invasions are important to study because the native biota can be seriously affected. Invasive plants are known to compete with and, in some cases, locally threaten native species (e.g., this study; see also Mulvaney 1986; Braithwaite et al. 1989; de Rouw 1991), alter ecosystem development (Vitousek et al. 1987; Vitousek and Walker 1989), and change bird communities (Esler 1990; Fraser and Crowe 1990). Furthermore, hybridization can often occur between native and invasive species (e.g., *C. monogyna* and *C. suksdorfii* at the study site: Love and Feigen 1978). Such hybridization contaminates the gene pool of native taxa and therefore conflicts with one of the primary goals of conservation biology.

Finally, the results presented here can be used to make useful management recommendations in a number of ways. Where *C. monogyna* co-occurs with native *Crataegus* species, it is clear that the invasive is a potential threat and should be managed against. Alternatively, the promotion of a native species that could compete well with *C. monogyna* (but that would not cause problems for *C. suksdorfii,* for example) may serve to short-circuit the dispersal, and

therefore, the reproductive success, of the invasive. In contrast, for those parties interested in bird conservation, management for *C. monogyna* (via ornamental plantings, hedgerows, etc.) may lead to an increase in frugivore populations, although any such management must proceed with caution.

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POLLINATION BIOLOGY OF *ASARUM HARTWEGII* (ARISTOLOCHIACEAE): AN EVALUATION OF VOGEL'S MUSHROOM-FLY HYPOTHESIS

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Abstract

Stefan Vogel proposed that flowers of *Asarum* s.l. mimic the fruiting bodies of fungi and are pollinated by flies whose larvae feed on mushrooms. Contrary to this view, the flowers of *A. hartwegii* are predominantly autogamous in the Klamath Mountains of northern California. Seed set of bagged flowers in one large population was equivalent to that of unmanipulated controls while emasculated flowers set only about 3% as many seeds as controls. Circumstantial evidence suggests, however, that the vectors responsible for the limited amount of allogamy are mycophagous flies lured by deception. We found fly eggs in 38% of more than 1100 flowers inspected over a four year period. The eggs belonged to 8 species in at least 4 families. The most abundant were laid by *Suillia thompsoni* (Heleomyzidae), whose larvae are obligately mycophagous. Two of the other three flies we identified, *Docosia* sp. (Mycetophylidae) and *Scaptomyza pallida* (Drosophilidae), also have mycophagous larvae while the larvae of the third species, *Hylemya fugax* (Anthomyiidae), normally feed on decaying plant material. Hatched eggs were common in the flowers, but we rarely saw larvae, implying that floral tissue is not a suitable larval substrate and that ovipositing females are attracted by deception. Evidence that the flies are pollinators comes from studies of emasculated flowers: those with eggs were more than three times as likely to set fruit as those without eggs.

Vogel (1973, 1978) described a class of flowers that appear to chemically and structurally mimic the fruiting bodies of fungi and thereby attract flies, especially fungus gnats, who normally oviposit on mushrooms. He proposed that the flies mate and lay eggs in the flowers, and in the process pollinate them. Since the larvae that emerge cannot feed on floral tissue, pollination is acquired by deception (Dafni 1984). Vogel identified several potential examples of such "pilzmüchenblumen", including members of the Araceae and Orchidaceae (see Meeuse and Morris 1984, p. 53, for a striking example), but most of the empirical evidence for the hypothesis came from his studies of *Asarum* and related genera (Aristolochiaceae). Some wild gingers, especially Asian species in the genus *Heterotropa,* have elaborate lamellar or reticulate sculpturing on their sepals that Vogel likened to gill and pore hymenophores, places where fungus gnats ordinarily lay their eggs.

Little is known about the pollination of *Asarum* and its close relatives. Fewer than 10 of the 100 or more species in the complex have been studied in the field, but it appears that at least some are

pollinated by ovipositing fungus gnats, in accord with Vogel's hypothesis (Sugawara 1988). Other species, however, are exclusively or predominantly autogamous (Wildman 1950; Werth 1951; Daumann 1972; Lu 1982; Tanaka and Yahara 1987). In this paper, we present the results of a four-year study of the pollination biology of *Asarum hartwegii* Wats. in California. Although its flowers are mostly self-pollinating, we argue that autogamy has been superimposed on a system fundamentally adapted for pollination by mycophagous flies.

Methods

Species and study sites. Asarum hartwegii is restricted to the understories of relatively open, mixed conifer-hardwood forests in the Klamath and Sierra Nevada Mountains of California (Mesler and Lu 1990). Unlike some other North American species in the genus (e.g., *A. caudatum, A. canadense*), which form extensive mat-like clones, individual plants of *A. hartwegii* occur as distinct clumps. Each plant bears from 1 to several concurrently blooming flowers at ground level. The flowers have reddish-brown sepals and produce a faint, musty fragrance. The bases of the sepals stand close together to form a false calyx tube. On the inner surface of the tube, each sepal bears several dense parallel bands of white hairs. The flowers are protogynous; stigmas are receptive for about seven days before anthers dehisce. At the close of the female stage, the filaments change orientation, so that first 6 (early-male stage) and then all 12 anthers (late-male stage) come into contact with stigmas. Lu (1982) and Tanaka and Yahara (1987) illustrate an essentially identical auto-pollination mechanism in two other species of *Asarum*. Ovule number ranges from 21 to 95 per flower (average = 53.2, SE = 0.9, n = 383).

Our main study site was Steelbridge campground, located 7 km SE of Weaverville, CA. (Trinity Co.). Here a large population of more than 1000 plants of *A. hartwegii* occurs in a relatively mesic Douglas Fir forest on a north-facing slope at 700 m. Additional observations were made at four other sites in northern California, the most distant approximately 80 km NE of Steelbridge (Trinity Co.: Cal Trans rest stop, 12.8 km E of Willow Creek; Gray's Falls Campground, 19.5 km E of Willow Creek; Denny Rd, 2.4 km N of CA 299; Shasta Co.: Ah-di-na Campground, 16 km S of McCloud).

Pollination experiments. Plants selected from throughout the Steelbridge site were used to assess the relative importance of autogamy, allogamy, and apomixis. A single flower per plant was assigned to one of the following pollination treatments. (1) *Controls*— Unmanipulated, open-pollinated flowers provided an estimate of

natural levels of fruit and seed production in 1984 and 1985. (2) *Emasculated*—To estimate the potential for allogamy during the female stage, we emasculated newly opened flowers in 1984, and then bagged them after 7 additional days of exposure. The bags were left on for 2–3 weeks, until the stigmas turned brown and were apparently no longer receptive. In 1985, flowers were emasculated in the same way but not bagged, to allow the maximum opportunity for detection of cross-pollination. In both 1984 and 1985, the average distance between emasculated flowers and the nearest male flower was less than 1 m, insuring a source of pollen for cross-pollination. Because the closest pollen source was often another flower on the same plant, seeds produced by emasculated flowers could result from either geitonogamous or xenogamous pollinations. (3) *Bagged*—To test for self-compatibility and the effectiveness of autopollination, we bagged a set of flowers in 1984 prior to anthesis. The bags were removed after the stigmas were no longer receptive. (4) *Emasculated and bagged*—To check for apomixis, we emasculated and bagged 13 flowers in 1984. The average number of ovules per flower did not differ significantly across treatments in either year (P's > 0.10).

Experimental flowers were collected prior to fruit maturation at the end of the season, after allowing enough time for maturing seeds to be unambiguously distinguished from unfertilized ovules and abortive seeds. We expressed pollination success on two levels, the percentage of flowers that set fruit and the average number of seeds per fruit. We calculated G and t statistics to test for differences in fruit set and seed number, respectively (Sokal and Rohlf 1981). In 1984, a priori pairwise tests were used to compare the performance of control vs. emasculated flowers and control vs. bagged flowers. Seed number was square-root transformed, as necessary, to equalize variances prior to statistical analysis. Emasculated flowers were checked for fly eggs and larvae, as described below, to determine the relationship between oviposition and pollination.

Surveys for fly eggs and larvae. To determine the frequency of flower visitation by ovipositing flies, additional flowers were checked for eggs and larvae at Steelbridge over a four-year period. In 1984–1986, sets of female, early male, and late male flowers were collected weekly throughout the flowering season. In 1987, collections were made at the end of the season when male-phase flowers predominated. Flowers from the other four study sites, most of which were in late male phase, were inspected for eggs and larvae in 1985 or 1986. In all cases, sepals were removed from flowers and examined at 30× as eggs are easily overlooked, especially the translucent ones of fungus gnats. Basidiocarps were uncommon at Steelbridge during the flowering season, but we checked those we found for fly eggs.

TABLE 1. COMPARISON OF FRUIT AND SEED PRODUCTION BY CONTROL, EMASCULATED, AND BAGGED FLOWERS. G-tests and t-tests were used to compare fruit set and seed number, respectively. [a] Control vs. emasculated, P < 0.001; control vs. bagged, P > 0.10. [b] Control vs. emasculated, P < 0.001. [c] Control vs. emasculated, P < 0.001; control vs. bagged, P > 0.90. [d] Control vs. emasculated, P < 0.001.

	Fruit set		Number of seeds per fruit	
	1984[a]	1985[b]	1984[c]	1985[d]
	% (N)	% (N)	$\bar{x} \pm$ SE (N)	$\bar{x} \pm$ SE (N)
Control	98.2 (111)	100 (58)	35.8 ± 1.5 (109)	34.3 ± 1.6 (58)
Emasculated	20.9 (115)	65.6 (99)	5.0 ± 1.1 (24)	17.3 ± 1.4 (65)
Bagged	100 (51)	—	35.1 ± 1.6 (51)	—

Flies were reared at room temperature in glass culture dishes with a 2–3 cm layer of slightly moistened vermiculite at the bottom, covered with a piece of filter paper. Eggs or larvae from the flowers were transferred to a piece of moistened substrate placed on top of the filter paper. We used pieces of unflavored rice cake or commercial mushroom as the substrate. Mushrooms used in the cultures were checked carefully in advance for eggs and larvae.

RESULTS

Mating system. None of the emasculated and bagged flowers set fruit, indicating that apomixis (agamospermy) does not occur. Very little allogamy occurred in 1984, as shown by the low fecundity of emasculated flowers, which produced only about 3% as many seeds as controls (Table 1). The difference was the result of both a higher percentage of fruit set on the part of control flowers and a greater average number of seeds per fruit. In contrast, fruit and seed sets of controls and bagged flowers were equivalent, indicating that autogamy was responsible for most seed production.

The stigmas of the flowers we emasculated and left unbagged in 1985 remained turgid and apparently receptive for several weeks. Not surprisingly, these flowers experienced a higher level of pollination success than the ones we emasculated in 1984 (Table 1). Nevertheless, fruit and seed sets of controls still greatly exceeded those of emasculated flowers.

Frequency of flower visitation and oviposition. During our four-year study at Steelbridge, we checked hundreds of flowers, from early morning to dusk. Adult insect visitors, which included fungus gnats, other flies (Heleomyzidae, Anthomyiidae), and a staphylinid beetle (*Anthobium* sp.), were present in far less than 1% of the flowers. In contrast, we consistently found fly eggs and larvae in them during the same four year period. The fraction of flowers with at least one

TABLE 2.   COMPARISON OF FRUIT AND SEED PRODUCTION BY EMASCULATED FLOWERS WITH AND WITHOUT FLY EGGS. G-tests and Mann-Whitney U-tests were used to compare fruit set and seed number, respectively.

	Fruit set		Number of seeds per fruit	
	1984	1985	1984	1985
	% (N)	% (N)	x̄ ± SE (N)	x̄ ± SE (N)
Eggs present	46.2 (26)	76.7 (73)	7.0 ± 2.1 (12)	18.3 ± 1.5 (56)
Eggs absent	13.5 (89)	34.6 (26)	3.1 ± 0.7 (12)	10.8 ± 3.5 (9)
	$P < 0.001$	$P < 0.001$	$P = 0.08$	$P = 0.03$

egg ranged from about 21% in 1984 to 59% in 1987 (Table 3). On average, flowers contained 2.6 to 4.0 eggs, depending on year, but the distribution was strongly skewed, with a single egg present in more than 35% of the cases. Ovipositing flies visited female, early male, and late male phase flowers, as shown by the increase in the percentage of flowers with eggs in successively older flowers (Fig. 1). More than 90% of the eggs were found on the inside of the calyx tube, between rows of hairs or beneath the hairs. Larvae were much less common than eggs (Table 3), even though collapsed (and presumably hatched) eggs were frequently seen. Larvae were usually found at the base of the flower, where they appeared to be eating pollen, not floral tissue.

We found the eggs of eight different species of flies in flowers at Steelbridge, four of which we were able to rear and identify (Table 3). The most common eggs are fusiform, 0.75–0.80 mm long, and have a reticulate, opaque white chorion. These belong to *Suillia thompsoni* (Heleomyzidae). Another higher fly, *Hylemya fugax* (An-

TABLE 3.   PERCENTAGE OF FLOWERS WITH FLY EGGS AND LARVAE. With few exceptions, larvae were those of higher flies (= lacked a head capsule).

	1984	1985	1986	1987
	Percentage			
Eggs				
Suillia thompsoni Gill (Heliomyzidae)	12.6	33.8	24.2	28.5
Hylemya fugax (Meigen) (Anthomyiidae)	5.1	5.4	9.0	29.2
Scaptomyza pallida				
Zetterstedt (Drosophilidae)	0.2	0.2	0.3	0.0
Docosia sp. (Mycetophilidae)	0.2	0.0	2.0	1.5
Unidentified fungus gnats	0.2	0.0	1.2	0.1
Other unidentified eggs	5.1	4.5	13.5	16.9
All egg types	20.9	40.4	45.8	58.5
Larvae	1.8	2.9	7.4	8.5
Number of flowers inspected	334	314	244	130
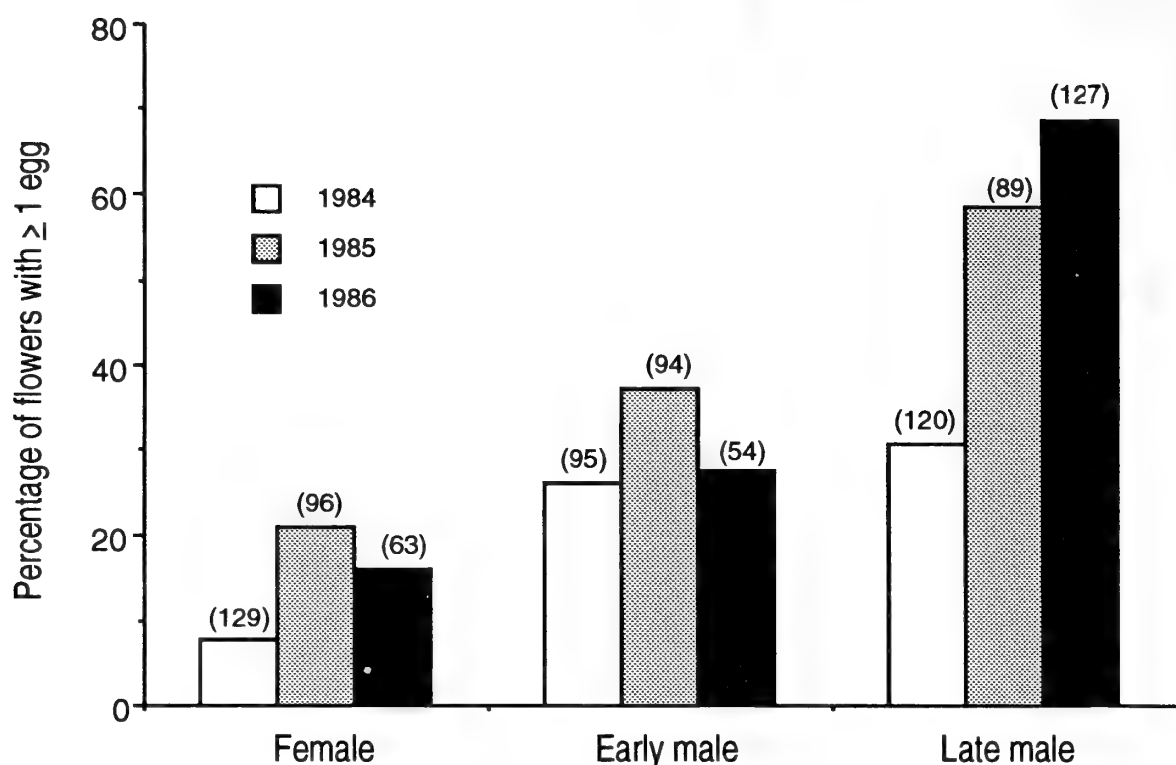
FIG. 1.   The percentage of female, early male, and late male flowers with ≥ 1 egg in 1984–1987 at Steelbridge. Numbers in parentheses are sample sizes.

thomyiidae), laid eggs in fewer flowers, except in 1987. The eggs of this species are similar to those of *S. thompsoni,* except for a pair of ridges that run down one side. Much less common were the eggs of the fungus gnat *Docosia* sp. (Mycetophylidae), which are smaller (0.3 mm long), ovoid, and have a translucent chorion with faint striations. We rarely found eggs of *Scaptomyza pallida* (Drosophilidae), which are 0.5 mm long, with a coarsely reticulate chorion and a pair of prominent wings. Among the unidentified eggs were two other types with the opaque, reticulate or striate chorion characteristic of higher flies, in addition to the elongate, translucent ones of other fungus gnats (Mycetophylidae or Sciaridae). We found eggs of *S. thompsoni* and fungus gnats on fruiting bodies of *Cortinarius* and *Collybia* collected at the site.

Fly eggs were present in 19% (n = 57), 50% (n = 12), 57% (n = 7), and 60% (n = 20) of the flowers inspected at the four other sites, respectively. In general, the same ensemble of eggs was found at these sites as at Steelbridge. *S. thompsoni* accounted for more than half of the ovipositions at all four of the sites. Among the other eggs were those of *H. fugax, Docosia* sp., *S. pallida,* and one of the unidentified higher flies seen at Steelbridge.

Relationship between oviposition and pollination. Although we occasionally saw flies on anthers and stigmas, we could not establish, by direct observation, a link between oviposition and pollination

because flower visits were so infrequent. Correlative evidence suggests, however, that ovipositors are pollinators. In both 1984 and 1985, emasculated flowers with eggs had a much higher probability of setting fruit than those without eggs (Table 2). The number of seeds per fruit was also higher for flowers with eggs in both years, although the difference was not significant in 1984. The number of seeds per flower was correlated with the number of eggs per flower in both years, although much more weakly so in 1984 (1984: Pearson r = 0.15, P = 0.06, n = 115; 1985: r = 0.49, P < 0.001, n = 99).

DISCUSSION

Our observations provide mixed support for Vogel's hypothesis that wild ginger flowers are adapted for pollination by mushroom flies. On the one hand, if our Steelbridge study site is representative, *A. hartwegii* is predominantly autogamous. The initial female floral phase allows for allogamy, but insect visits are very infrequent and automatic self-pollination is responsible for nearly all seed production. Other species of *Asarum* s.s. likewise appear to be mostly or completely autogamous (Wildman 1950; Werth 1951; Daumann 1972; Lu 1982; Tanaka and Yahara 1987). On the other hand, our emasculations revealed a limited amount of pollen transfer between flowers. We did not witness cross-pollination, but strong circumstantial evidence suggests that the pollen vectors are ovipositing flies lured to the flowers by deception: (a) flies commonly visit and lay eggs in both female- and male-phase flowers, (b) their larvae do not eat floral tissue, and (c) emasculated flowers with eggs are much more likely to be pollinated than those without eggs. An analysis of the larval substrates normally used by the flies is consistent with the idea that the deception is based on mimicry of fungi, as Vogel proposed.

Three of the four flies whose eggs we could identify have mycophagous larvae. The most common egg-layer, and presumably the most important pollinator, *S. thompsoni* (Heleomyzidae), is an obligate mycophage which oridinarily oviposits on the fruiting bodies of several genera of fungi (Hayward 1984; R. S. LaChance unpublished data). We found its eggs on *Cortinarius* and *Collybia* at Steelbridge. *Docosia* sp. and other, unidentified Mycetophilidae or Sciaridae also oviposited in the flowers, although much less frequently than *Suillia*. Members of this group are well-known fungivores (Vockeroth 1981). Like many other fruit flies, *S. pallida* is mycophagous, although its larvae are known to use decaying plant material also (Dely-Draskovits and Papp 1973; Courtney et al. 1990). The fourth species, *Hylemya fugax,* apparently has not been collected from mushrooms. Its larvae use a wide variety of substrates, but they prefer decaying plant material (Miles 1950). Other saprophagous flies are known to

use mushrooms as a food source (Bruns 1984), and the same may be true of *H. fugax,* especially since two other species of *Hylemya* are so-called secondary fungivores (Eisfelder 1956; Bruns 1984), ones that specialize on decomposing mushrooms.

Even though *A. hartwegii* is almost exclusively autogamous, its flowers have features, like protogyny, elaborate sepals, and fragrance, that probably evolved as part of an insect-pollinated system. If these traits are, in fact, adaptations for cross-pollination by mycophagous flies, they are largely vestigial at present. The same may be true of the obviously entomophilous features of *A. caudatum,* the species which Vogel (1978) used as the centerpiece of his work on the fungal mimesis hypothesis. Although he observed pollination of this species by ovipositing fungus gnats in his garden in Europe, and found mycetophilid eggs in flowers from several populations in western North America, Lu (1982) showed that *A. caudatum,* like *A. hartwegii,* is primarily autogamous. The apparent loss of the interaction responsible for the evolution of the traits of *A. hartwegii* and *A. caudatum* makes testing Vogel's hypothesis difficult or impossible in these cases. Studies of other members of the *Asarum* s.l. complex, most of which cannot directly self-pollinate and thus must rely on insects for pollination (Sugawara 1987), would provide more convincing tests of the hypothesis. The single species in this group that has been studied, *Heterotropa tamaensis,* is pollinated by ovipositing fungus gnats (Sugawara 1988).

Vogel's hypothesis that certain flowers obtain pollination by masquerading as mushrooms is worthy of further study. Our results indicate, however, that the hypothesis should be extended to include potential pollinators other than Mycetophylidae. Flies in several families, including Anthomyiidae, Drosophilidae, Heleomyzidae, Muscidae, and Phoridae, lay their eggs on mushrooms (see references in Bruns 1984). Moreover, the feeding habits of mycophagous fly larvae are diverse; some prefer fresh, living tissue while others use decomposing mushrooms (Eisfelder 1956; Bruns 1984; Hayward 1984). Given this diversity, we should expect a range of different mushroom-fly blossoms, depending on the larval preferences of the flies involved. Some, in fact, may rely exclusively on fungus gnats (e.g., *Heterotropa tamaensis,* Sugawara 1988) but others, like *A. hartwegii,* may have evolved as more generalized mushroom mimics that attract an array of mycophagous flies.

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NEW VASCULAR PLANT RECORDS AND THE
INCREASE OF EXOTIC PLANTS IN
GLACIER NATIONAL PARK, MONTANA

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ABSTRACT

We report 39 additions to the flora of Glacier National Park. Fourteen of these are exotic weeds. Both the number of exotics and visitors have increased at an accelerating rate since 1920. These findings suggest that control of exotics will be an increasingly difficult task for managers of popular reserves.

Congress established Glacier National Park (GNP) in 1910. In 1919 Paul Standley conducted the first systematic botanical survey and published the results in *Flora of Glacier National Park, Montana* (Standley 1921). Since then botanical studies and collecting have been sporadic (see references in Lesica 1985). During the 1950's and 1960's LeRoy Harvey and his students at the University of Montana collected extensively in Glacier National Park and discovered many new additions (Harvey 1954; Bamberg and Pemble 1968). Published reports and specimens housed in the Glacier National Park herbarium served as the sources for a recent checklist of the park's flora (Lesica 1985). Since then, we and a number of park employees have collected many new records. In addition, some records have been found in herbaria at the University of Montana (MONTU) and Montana State University (MONT). Here we report 39 additions to the flora of Glacier National Park. Reports of *Barbarea vulgaris, Cardamine oligosperma* var. *kamtschatica, Carex tenuiflora, Draba macounii, Petasites frigidus, Sagina nivalis,* and *Satureja vulgaris* have been published previously (Lesica et al. 1986; Lackschewitz et al. 1988; Lesica 1991). Nomenclature follows Hitchcock and Cronquist (1973). Specimens housed at the Glacier National Park herbarium in West Glacier are followed by (GNP).

Fourteen (36%) of the species reported here are introduced Eurasian weeds (preceded by an asterisk). By 1920 at least 57 species of exotics were already present (Standley 1921). Since then, this number has increased steadily. At the same time, the number of

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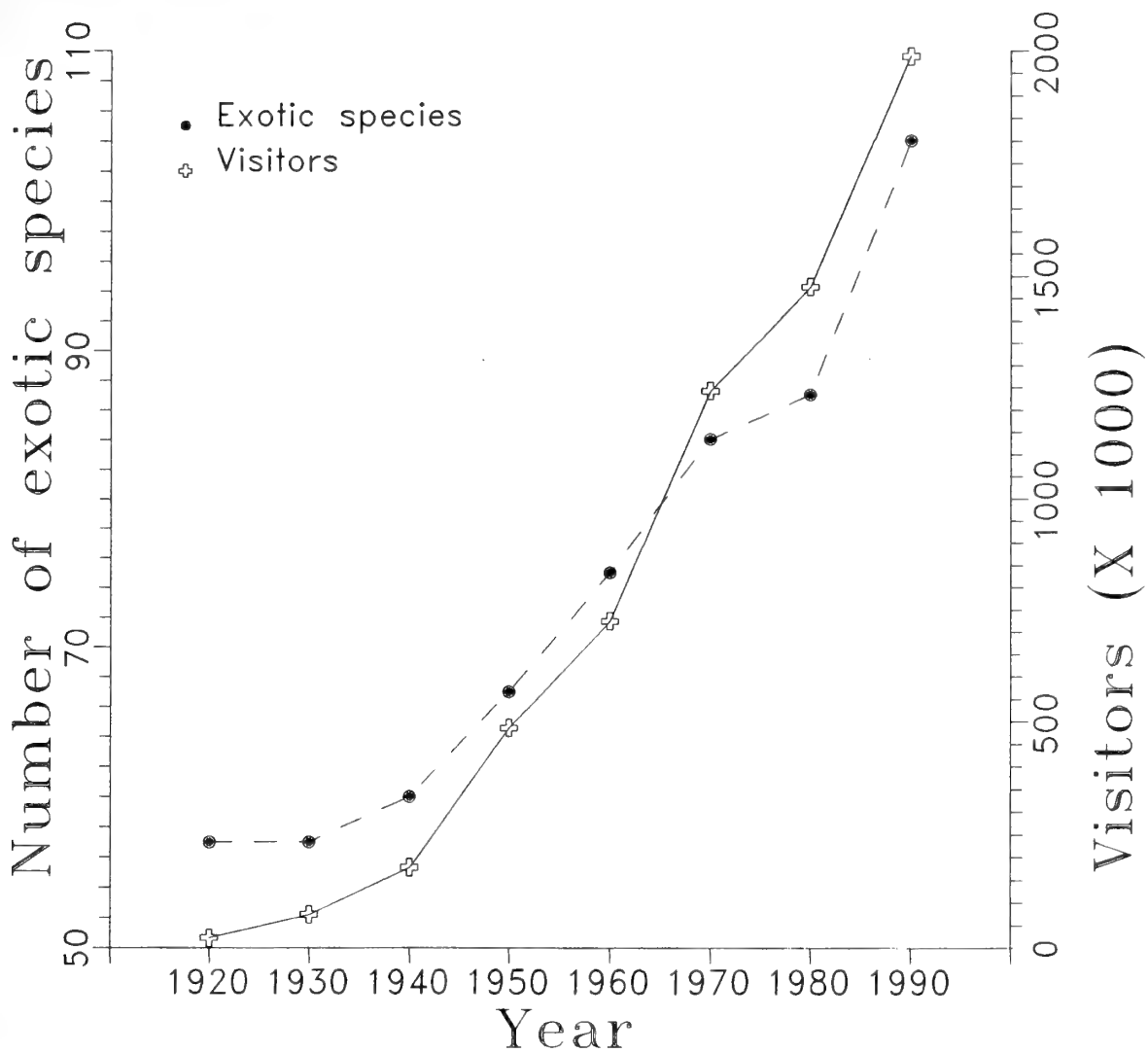
FIG. 1.   Number of exotic plant species occurring in Glacier National Park based on herbarium records and published literature and number of visitors to GNP based on official records since 1920.

visitors to the park has also increased. Most of this visitation is by automobile, one of the most common vectors for the transport of exotic weeds (Baker 1972; Sauer 1988; Tyser and Worley 1992). The strong correlation between increasing visitation and the increasing number of exotics (Fig. 1) suggests that invasion by weeds will continue to be a problem to managers of high-profile reserves. Monitoring the success of new invaders will be an increasingly important part of resource management in these reserves.

Agropyron scribneri Vasey (Poaceae).—Glacier Co., windswept ridge NW of Poia Lake, common in limestone shingle with *Eriogonum androsaceum* and *Potentilla fruticosa,* 2469 m, 6 Jul 1985, *P. Lesica 3502* (GNP).

Antennaria pulcherrima (Hook.) Greene (Asteraceae).—Glacier Co., S edge of Lunch Creek cirque ca. 1.2 km NE of Logan Pass, locally common in moist tundra with *Carex scirpoidea* and *C. capillaris,* 2164 m, 10 August 1989, *P. Lesica and B. McCune 4963* (ALTA, MONTU); same location, 8 Aug 1990, *P. Lesica 5225* (GNP, MONTU) (collections verified by R. Bayer, ALTA).

Arenaria serpyllifolia L. (Caryophyllaceae).—Flathead Co., West Glacier, Park head-quarters, common in compacted soil just N of garage area with *Potentilla argentea* and *Poa annua,* 945 m, 3 Jun 1986, *P. Lesica 3762* (GNP, MONTU).

Artemisia absinthium L. (Asteraceae).—Flathead Co., along Hwy 2 near Middle Fork Flathead River ca. 4.8 km S of Walton Ranger Station, uncommon in gravelly soil with *Dactylis glomerata* and *Iliamna rivularis,* T29N R15W S30, 1250 m, 10 Jul 1991, *P. Lesica 5483* (GNP, MONTU); West Glacier, along footpath between maintenance yard at park headquarters and Middle Fork Flathead River with *Agrostis alba* and *Melilotus officinalis,* 975 m, 23 Aug 1991, *P. Lesica 5597* (GNP, MONTU).

Bromus commutatus Schrad. (Poaceae).—Flathead Co., Lake McDonald, disturbed area along creek, in gravel, 975 m, 2 Jul 1942, *W. Booth s.n.* (GNP, MONT); S-facing slopes of Apgar Mountain just N of the Middle Fork Flathead River, locally common in shallow, rocky soil with *Agropyron spicatum* and *Epilobium paniculatum,* T31N R19W S5 NE¼, 1097 m, 9 Jul 1990, *P. Lesica 5152* (GNP).

Campanula glomerata L. (Campanulaceae).—Flathead Co., SW end of Ruhle Drive in the residence area at West Glacier, in a meadow with *Bromus inermis* and *Chrysanthemum leucanthemum,* 945 m, 2 Jul 1986, *P. Lesica and A. DeBolt 3924* (GNP).

Carex concinna R. Br. (Cyperaceae).—Flathead Co., along N shore of Kintla Lake, shaded site, 25 May 1979, *J. Beehler 58* (MONTU); North Fork Flathead River, locally common in mossy soil beneath spruce trees on a gravelly shore with *Viola adunca* and *Fragaria virginiana,* T36N R21W S31 NE¼, 1122 m, 10 Jun 1988, *P. Lesica 4562* (GNP, MONTU); along the inside road ca. 0.3 km S of Ford Creek, locally common in wet, marshy soil, in a seep area with *Carex capillaris* and *Linnaea borealis,* T36N R21W S19, 1134 m, 10 Jun 1988, *P. Lesica 4564* (GNP, MONTU).

Centaurea jacea L. (Asteraceae).—Flathead Co., Bowman Lake area, S of picnic area, approx. 0.65 ha of knapweed, T35N R20W S5, 1228 m, 2 Sep 1989, *G. Vodehnal s.n.* (GNP).

Crepis tectorum L. (Asteraceae).—Flathead Co., disturbed area in a lawn at Polebridge Ranger Station along North Fork Flathead River, 1100 m, 20 Aug 1983, *J. DeSanto s.n.* (GNP).

Dianthus armeria L. (Caryophyllaceae).—Glacier Co., Lubec area, roadside near railroad near Firebrand Pass trailhead, 22 Aug 1989, *J. DeSanto s.n.* (GNP).

Dicentra uniflora Kell. (Fumariaceae).—Flathead Co., Blacktail Hills area, dry S-facing slopes, 1630 m, 16 Apr 1992, *J. DeSanto s.n.* (GNP).

Draba verna L. (Brassicaceae).—Flathead Co., along the Middle Fork of Flathead River near the old bridge ca. 0.2 km upstream of the residence area, uncommon in moist open soil of rock outcrops growing in moss, 945 m, 5 May 1985, *P. Lesica and A. DeBolt 3307* (GNP); same location, 3 May 1991, *P. Lesica 5293* (GNP, MONTU).

Eleocharis pauciflora (Lightf.) Link (Cyperaceae).—Flathead Co., ca. 0.3 km NW of Mt. Reynolds, ca. 1.2 km S of Logan Pass, locally common in muddy, thin soil of seepy areas on rock shelves with *Juncus triglumis* and *Carex nigricans,* 2255 m, 2 Aug 1987, *P. Lesica and K. Ahlenslager 4457* (GNP, MONTU); —Glacier Co., Mt. Reynolds, Logan Pass, wet tundra terrace, 9 Aug 1960, *W. B. Schofield s.n.* (MONTU); cirque on E side of Mt. Reynolds, ca. 1.2 km S of Logan Pass, common in wet mud of a seep area on a bench with *Juncus mertensianus* and *Tofieldia glutinosa,* 2255 m, 9 Aug 1988, *P. Lesica and K. Ahlenslager 4715* (GNP, MONTU).

Epilobium palustre L. (Onagraceae).—Flathead Co., "Moose Meadow", open *Carex* marsh, T33W R19W S18, 7 Jul 1969, *M. Mooar 10911* (MONTU); *Typha* marsh, small pool in forest of mixed conifers and birch, T34N R20W S35, 8 Jul 1969, *M.*

Mooar 10982 (MONTU); S end of McGee's meadow, common in wet organic soil with *Carex lasiocarpa* and *C. buxbaumii,* 1219 m, 4 Jul 1985, *P. Lesica 3481* (GNP).

Erigeron ochroleucus Nutt. (Asteraceae).—Glacier Co., Chief Mountain, dry slopes, 1951 m, 26 Jun 1989, *J. DeSanto s.n.*; Chief Mountain, open dry slopes, 2057 m, 26 Jun 1990, *J. DeSanto s.n.* (GNP).

*Erodium cicutarium (L.) L'Her. (Geraniaceae).—Glacier Co., a few plants along the road ca. 5 km W of east entrance, 1385 m, 23 Jun 1963, *W. E. Booth 63122* (MONT); Flathead Co., disturbed area at Polebridge Ranger Station, 1100 m, 26 May 1983, *Jerry DeSanto s.n.* (GNP); disturbed ground in maintenance area by Park headquarters. West Glacier, 975 m, 10 Jun 1986, *A. DeBolt s.n.* (GNP).

Juncus tenuis Willd. (Juncaceae).—Flathead Co., "Moose Meadow", open *Carex* marsh, T33N R19W S18, 7 Jul 1969, *M. Mooar 10910* (MONTU); wet meadows, 1951 m, 29 Aug 1977, *P. Zager s.n.* (MONTU); along McDonald Creek ca. 0.2 km below the outlet of McDonald Lake, common in moist gravelly soil with *Rorippa islandica* and *Agrostis alba,* 960 m, 8 Sep 1985, *P. Lesica 3680* (GNP, MONTU); — Glacier Co., along trail to Firebrand Pass ca. 1.5 km NW of Lubec Lake, common in lodgepole pine forest with *Agrostis exarata* and *Deschampsia elongata,* 1676 m, 9 Aug 1991, *P. Lesica 5577* (GNP, MONTU).

Lewisia rediviva Pursh (Portulacaceae).—Blacktail Hills (also across Highway 2 in Flathead National Forest), dry open slopes, 1554 m, 29 Jun 1989, *J. DeSanto s.n.* (GNP).

Linanthus septentrionalis Mason (Polemoniaceae).—Flathead Co., Blacktail Hills, dry S-facing slope, 1615 m, 24 Jun 1990, *J. DeSanto s.n.* (GNP); —Glacier Co., steep S-facing slope NW of Poia Lake with *Saxifraga bronchialis* and *Potentilla glandulosa,* common in rocky soil, 2134 m, 6 Jul 1985, *P. Lesica 3503* (GNP, MONTU).

*Lolium multiflorum Lam. (Poaceae).—Flathead Co., old roadway along the N side of Middle Fork Flathead River just below residence area, T32N R19W S36, 975 m, 9 Jul 1990, *P. Lesica 5155* (GNP, MONTU).

*Lomatium cous (Wats.) Coult. & Rose (Apiaceae).—Flathead Co., bare slopes and ridges, 1700 m, 4 May 1992, *J. DeSanto & R. Mattson s.n.* (GNP).

*Medicago lupulina L. (Fabaceae).—Glacier Co., scattered plants in disturbed area at the east entrance, 1385 m, 14 Jun 1952, *W. E. Booth s.n.* (MONT).

*Myosotis scorpioides L. (Boraginaceae).—Flathead Co., along the Middle Fork Flathead River just upstream of West Glacier bridge, common in open cedar-spruce forest with *Aralia nudicaulis* and *Disporum trachycarpum,* 945 m, 1 Jun 1985, *P. Lesica 3343* (MONTU).

Ophioglossum vulgatum L. (Ophioglossaceae).—Flathead Co., S side of and between Howe Lakes, local and uncommon in a moist meadow with *Botrychium multifidum* and *Lycopus uniflorus,* 1250 m, 2 Sep 1988, *P. Lesica 4745* (GNP, MONTU).

Orobanche fasciculata Nutt. (Orobanchaceae).—Flathead Co., Blacktail Hills, open dry hillside, 1676 m, 5 Jul 1990, *J. DeSanto s.n.* (GNP); —Glacier Co., Napi Point, dry open slopes, 1981 m, 29 Jul 1989, *J. DeSanto s.n.* (GNP).

Polygonum kelloggii Greene (Polygonaceae).—Glacier Co., lower end of Preston Park near treeline ca. 1.8 km NE of Logan Pass, abundant in open soil of a late snowmelt-temporary pond area with *Senecio cymbalarioides* and *Juncus mertensianus,* 2164 m, 10 Sep 1987, *P. Lesica 4513* (GNP, JEPS, MONTU) (collection verified by J. Hickman, JEPS).

Potentilla ovina Macoun (Rosaceae).—Glacier Co., near east entrance, roadside, rocky outcrop, 15 August 1942, *W. E. Booth s.n.* (MONT); Piegan Mtn., Logan Pass, rocky

talus, 1970 m, 27 Jul 1954, *L. Harvey 6089a* (MONTU); Divide Mtn., NW slope of peak near treeline associated with scattered krumholz, 2150 m, 26 Jun 1964, *L. Harvey and R. Pemble 7046* (MONTU); windswept ridge NW of Poia Lake, common in limestone shingle with *Eriogonum androsaceum* and *Potentilla fruticosa,* 2469 m, 6 Jul 1985, *P. Lesica 3497* (GNP, MONTU); *Harvey 6089a* and *Harvey and Pemble 7046* verified by B. Johnston (COLO).

Potentilla recta L. (Rosaceae).—Flathead Co., West Glacier at intersection of Going-to-the-Sun Road and drive to residence area, small population in gravelly soil along road with *Centaurea maculosa* and *Linaria vulgaris,* T32N R19W S26, 975 m, 8 Aug 1991, *P. Lesica 5574* (GNP, MONTU).

Ranunculus abortivus L. (Ranunculaceae).—Flathead Co., confluence of McDonald Creek and Middle Fork of Flathead River, T32N R19W S27, 14 Jun 1968, *M. Mooar 8090* (MONTU); Logging Creek Ranger Station, common in parking area, 1048 m, 7 Jun 1985, *A. DeBolt 525* (GNP).

Ranunculus acris L. (Ranunculaceae).—Glacier Co., 2.7 km N of Belly River Ranger Station on old wagon road, in grass meadows, 10 Jul 1986, *D. Shea s.n.* (GNP); along small drainages flowing into Swiftcurrent Creek just below the lake near the horse trail, common with *Poa compressa* and *Trifolium repens,* 1460 m, 19 Jul 1987, *P. Lesica and K. Ahlenslager 4410* (GNP, MONTU); at entrance to Many Glacier campground near telephone booth just W of the residence area, small colony with *Poa pratensis,* 1494 m, 8 Jul 1990, *P. Lesica and K. Ahlenslager 5143* (GNP, MONTU).

Ranunculus cardiophyllus Hook. (Ranunculaceae).—Glacier Co., W edge of Belly River Ranger Station pasture, native bunchgrass meadow, 7 Jun 1988, *D. Shea s.n.* (GNP).

Ranunculus pygmaeus Wahlenb. (Ranunculaceae).—Glacier Co., N-facing cliff on Mt. Kipp, common in moist gravelly soil with *Salix arctica* and *Carex bipartita,* 2377 m, 3 Aug 1985, *P. Lesica & A. DeBolt 3602* (GNP, MONTU); W side of Mt. Reynolds ca. 0.6 km S of Logan Pass, scattered in wet boggy soil in seepy areas on rock shelves with *Tofieldia pusilla* and *Saxifraga debilis,* 2316 m, 2 Aug 1987, *P. Lesica and K. Ahlenslager 4453* (GNP, MONTU).

Sanguisorba occidentalis Nutt. (Rosaceae).—Flathead Co., West Glacier, Park headquarters, locally common in compacted soil N of garage area with *Poa annua* and *Potentilla argentea,* 945 m, 13 Jun 1986, *P. Lesica and A. DeBolt 4131* (GNP, MONTU).

Sanicula graveolens Poepp. (Apiaceae).—Flathead Co., Blacktail Hills, rocky wet slopes, 1524 m, 16 Jun 1990, *J. DeSanto s.n.* (GNP); S-facing slopes of Apgar Mountain just N of the Middle Fork Flathead River, locally common in shallow, rocky soil with *Agropyron spicatum* and *Epilobium paniculatum,* T31N R19W S5 NE¼, 1219 m, 9 Jul 1990, *P. Lesica 5153* (GNP, MONTU).

Saxifraga oregana Howell var. *subapetala* (A. Nels.) Hitchc. (Saxifragaceae.—Flathead Co., Blacktail Hills, damp open slopes among Douglas-fir with *Erythronium grandiflorum* and *Polygonum bistortoides,* 1753 m, 16 Jun 1990, *J. DeSanto s.n.* (GNP).

Senecio pauperculus Michx. (Asteraceae).—Flathead Co., trail to Kootenai Lake, old sphagnum bog with small stream through it, T37N R18W, 29 Jul 1966, *M. Mooar 2977* (MONTU); wet area near Polebridge, small stream and marshy area, T35N R21W S21, 1 Jul 1969, *M. Mooar 10700* (MONTU); bench just N of Trail Creek, ca. 0.9 km W of North Fork Road with *Pinus contorta,* T37N R22W S34, 1219 m, 22 Jul 1977, *P. Zager s.n.* (MONTU); 0.6 km S of Goat Haunt Ranger Station, wet marsh, 27 Jul 1990, *J. DeSanto s.n.* (GNP).

Senecio streptanthifolius Greene (Asteraceae).—Glacier Co., on top of Milk River Ridge above Cutbank Ranger Station near boundary of Glacier National Park, 3 Jul 1953, *J. McMullen 1055* (MONTU); Cutbank Ranger Station meadow, 3 Jul 1955, *R. Person s.n.* (MONTU); steep N-facing slope just S of Poia Lake, common in limestone talus with *Potentilla fruticosa* and *P. nivea,* 2012 m, 5 Jul 1985, *P. Lesica 3487* (GNP, MONTU).

*Veronica arvensis L. (Scrophulariaceae).—Flathead Co., West Glacier, Park head-quarters, common in compacted soil just N of garage area with *Potentilla argentea* and *Poa annua,* 945 m, 3 Jun 1986, *P. Lesica 3760* (GNP, MONTU).

Viola purpurea Kell. var. *venosa* (Wats.) Brain. (Violaceae).—Flathead Co., Blacktail Hills, dry S-facing slope with *Erythronium* and *Claytonia,* 1676 m, 5 Jun 1990, *J. DeSanto s.n.* (GNP).

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NOTEWORTHY COLLECTIONS

ARIZONA

CAREX MICRODONTA Torr. & Hook. (CYPERACEAE). — Cochise Co., Peterson Ranch (site), Scotia Canyon, Huachuca Mountains, T23S, R19E, sect. 3, with *Scirpus acutus, Lythrum californicum, Sisyrinchium demissum,* ca. 1860 m, 30 Jun 1991, *McLaughlin 6404* (ARIZ).

Previous knowledge. LA, MO, MS, OK, TX.

Significance. First record for AZ. Verified by Miriam E. Fritts.

CAREX PLANOSTACHYS Kunze (CYPERACEAE). — Cochise Co., Scheelite Canyon, Huachuca Mountains, with *Acer neomexicanum, Pseudotsuga menziesii, Quercus hypoleucoides,* ca. 1770 m, 7 May 1991, *Bowers 3483* (ARIZ). Determined by Miriam E. Fritts.

Previous knowledge. TX; MEXICO, San Luis Potosi; GUATEMALA.

Significance. First record for AZ.

COLOGANIA PALLIDA Rose (FABACEAE). — Cochise Co., Bear Canyon, Huachuca Mountains, 28 Sep 1949, Goodding 820-49 (ARIZ); Wakefield Camp, Huachuca Mountains, T23S R20E, sect. 30, with *Arbutus arizonica, Juniperus deppeana, Quercus arizonica,* ca. 1790 m, 2 Sep 1990, *Bowers 3340* (ARIZ); Yaqui Canyon, Huachuca Mountains, T24S, R20E, sect. 14, with *Quercus arizonica, Rhus trilobata,* ca. 1735 m, 17 Sep 1991, *Bowers 3590* (ARIZ). Santa Cruz Co., Josephine Canyon, Santa Rita Mountains, 23 Aug 1977, *Kaiser 1083a* (ARIZ). Greenlee Co., 9 mi N Hannagan Meadow, White Mountains, ca. 2650 m, 12 Aug 1935, *Kearney & Peebles 12442* (ARIZ).

Previous knowledge. NM, TX; MEXICO, Coahuila.

Significance. Addition to the flora of AZ. Early collections had been erroneously identified as *Cologania pulchella (Kearney & Peebles 12442)* and *Phaseolus heterophyllus (Goodding 820-49).*

HEXALECTRIS WARNOCKII Ames & Correll (ORCHIDACEAE). — Cochise Co., Oversite Canyon, Huachuca Mountains, T23S, R20E, sect. 33, with *Platanus wrightii, Amorpha fruticosa, Quercus arizonica, Q. hypoleucoides,* ca. 1890 m, 3 Sep 1990, *Bowers 3347* (ARIZ).

Previous knowledge. Cochise Co., Rhyolite Canyon, Chiricahua National Monument, Chiricahua Mountains, 1645 m, 24 Aug 1974, *Reeves R1214* (ASU); MEXICO, Baja California Sur.

Significance. Second locale for AZ and a westward range extension of 75 km.

STYLOSANTHES HUMILIS H.B.K. (FABACEAE). — Cochise Co., Bear Canyon, Huachuca Mountains, T23S, R19E, sect. 36, with *Muhlenbergia arizonica, Gutierrezia wrightii,* ca. 1680 m, 4 Nov 1990, *McLaughlin 6162* (ARIZ).

Previous knowledge. MEXICO: Chiapas, Colima, Guerrero, Jalisco, México, Oaxaca, Vera Cruz; CENTRAL AMERICA; CUBA; VENEZUELA.

Significance. First record for AZ; first record for the United States.

VIGUIERA MULTIFLORA (Nutt.) Blake var. MACROCEPHALA (Heiser) B. Turner (ASTERACEAE). — Cochise Co., Bear Canyon, Huachuca Mountains, T23S, R20E, sect. 29, with *Pseudotsuga menziesii, Aralia racemosa,* ca. 2010 m, 29 Sep 1991, *Bowers 3606* (ARIZ).

Previous knowledge. MEXICO, Chihuahua.
Significance. First record of this var. for AZ; first record for the United States.

—JANICE E. BOWERS, U.S. Geological Survey, 1675 W. Anklam Rd., Tucson, AZ 85745; and Steven P. McLaughlin, Office of Arid Lands Studies, University of Arizona, Tucson, AZ 85721.

CALIFORNIA

BACCHARIS VANESSAE Beauchamp (ASTERACEAE).—San Diego Co., CA, southern Santa Ana Mountains, San Mateo Canyon Wilderness Area of the Cleveland National Forest; lower end of Devil Canyon near the boundary with Camp Pendelton Marine Corps Base, T8S R6W SE corner S12, ca. 190 m. Northerly exposure, on open rocky outcrops of Santiago Peak volcanics above Devil Canyon riparian strip; associated with *Dudleya viscida, Polygala cornuta* ssp. *fishiae, Jepsonia parryi, Madia gracilis,* and *Pentagramma triangularis.* Surrounding vegetation of dense chaparral dominated by *Ceanothus spinosus, C. crassifolius,* and *Adenostoma fasciculatum.* 2 Oct 1992, *Boyd, Ross, and Mistretta 7711* (pistillate) & *7712* (staminate) RSA.
Previous knowledge. This rare shrub has previously been considered endemic to a narrow band of central-coastal San Diego County, from Encinitas eastward to Woodson Mountain, near Poway and southward to Mira Mesa; an area of ca. 30 km E-W by 17 km N-S.
Significance. A range extension northward of ca. 54 km. Presently listed as Endangered by the State of California, and being considered for similar listing under the federal Endangered Species Act. Its rarity is due to habitat loss through urbanization. Eight to twelve individuals were observed at the site of this newly discovered population and additional populations may be present in adjacent areas of the San Mateo Canyon Wilderness Area and Camp Pendelton Marine Corps Base.

—STEVE BOYD, TIMOTHY ROSS, and ORLANDO MISTRETTA, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

CALYCANTHUS OCCIDENTALIS Hook. & Arn. (CALYCANTHACEAE).—San Diego Co., Palomar Mts., Hwy S6 across from entrance to Fry Creek Campground, near 33°20′39″N, 116°52′44″W, T9S R1E sect. 33 SE¼ SE¼, 1500 m, montane coniferous forest with *Calocedrus decurrens, Pseudotsuga macrocarpa, Quercus chrysolepis,* and *Q. kelloggii,* 28 Jun 1990, *Suzanne Bell 44* (SD); same locality, 16 Sep 1992, *Levin 2222* (SD).
Previous knowledge. Sierra Nevada from Tulare Co. to Shasta Co. and in the Coast Ranges from Napa Co. to Trinity Co.
Significance. First record for southern California, a range extension of ca. 400 km SSE from Tulare Co.
Because *C. occidentalis* is sometimes cultivated and a variety of cultivated plants are established in the Palomar Mts. along hwys S6 and S7, human introduction of *C. occidentalis* into San Diego County cannot be ruled out. When she first collected it in 1990, Bell (label data) found just two plants. An extensive search in September 1992 revealed several small plants near the plants Bell found and one large plant across the highway, suggesting that the species is spreading and possibly was only recently established at this site. No other exotic plants grow near this site, however, nor is it a likely spot for someone to plant anything. In any case, *C. occidentalis* is well established and reproducing in the Palomar Mts.

CEPHALANTHERA AUSTINAE (A. Gray) A. A. Heller (syn. *Eburophyton austinae* (A. Gray) A. A. Heller) (ORCHIDACEAE).—San Diego Co., Hot Springs Mountain, Los

Coyotes Indian Reservation, along main road to summit ca. 0.1 mi S of "Rough Road" (alternate summit road), near 33°18'02"N, 116°33'19"W, T10S R4E sect. 15 NW¼ SW¼, 1830 m, rare in duff under oaks (*Quercus chrysolepis, Q. kelloggii*) in montane coniferous forest, 17 Jul 1992, *Levin 2220* (SD).

Previous knowledge. Sierra Nevada from Fresno Co. and in the Coast Ranges from Monterey Co. north to WA and ID.

Significance. First record for San Diego Co. and for the Peninsular Ranges, a range extension of ca. 120 km SE from near Lake Gregory, San Bernardino Mountains, where the species may be extirpated due to development (R. A. Coleman, personal communication).

—GEOFFREY A. LEVIN, see below.

STIPA CALIFORNICA Merr. & Burtt Davy in H. M. Hall (POACEAE).—San Diego Co., Cuyamaca Mts., Cuyamaca Peak, E slope, occasional along Burnt Pine Fire Rd ca. 250 m SE of jct with Conejos Trail, near 32°56'40"N, 116°35'55"W, T14S R4E unsect., 1800 m, in open areas with *Pinus coulteri, P. lambertiana, Arctostaphylos pringlei, Ceanothus palmeri, Bromus orcuttianus,* and *Elymus glaucus,* 21 Jul 1987, *Curto 409* (SD).

Previous knowledge. Previously known north from Riverside Co., CA to WA and ID.

Significance. First record for San Diego Co., a range extension of ca. 95 km south from the San Jacinto Mts., Riverside Co.

Field investigations since this first collection have found this grass to be fairly common on the east slope of Cuyamaca Peak, especially above 1800 m elevation; it has yet to be located elsewhere in San Diego County.

STIPA OCCIDENTALIS Thurb. in S. Wats. (POACEAE).—San Diego Co., Laguna Mts., ca. 200 m E of Horse Heaven Group Camp, local on N-facing rock outcrop along S side of un-named, seasonal tributary to Little Laguna Lake, near 32°53'09"N, 116°26'22"W, T15S R5E sect. 11 NE¼ NW¼, 1710 m, with *Pinus coulteri, Agrostis diegoensis, A. exarata, Bromus sitchensis, Deschampsia danthonioides, Elymus elymoides, E. glaucus, Festuca microstachys, Koeleria pyramidata, Monardella nana, Muhlenbergia rigens, Poa secunda, Stipa coronata,* and *S. lemmonii,* 24 Jun 1992, *Curto 834 and Allen* (SD).

Previous knowledge. Previously known north from Riverside Co., CA to WA and ID, and east to UT.

Significance. First collection for San Diego Co., a range extension of ca. 80 km south from the Santa Rosa Mts., Riverside Co.

—MICHAEL CURTO, see below.

HELIANTHELLA CALIFORNICA A. Gray var. NEVADENSIS (E. L. Greene) Jepson (ASTERACEAE: HELIANTHEAE).—San Diego Co., Volcan Mts., ca. 8 km (air) NNE of Julian, head of Arkansas Canyon, near 33°08'N, 116°34'50"W, T12S R4E sect. 8 SE¼ SE¼, 1620 m, infrequent in tree-encircled clearings on E-facing slope with *Calocedrus decurrens, Pinus coulteri, Quercus chrysolepis, Q. kelloggii, Bromus sitchensis, Elymus glaucus, Koeleria pyramidata, Poa howellii, P. secunda,* and *Monardella nana,* 23 June 1992, *Michael Curto 832, with Linda Allen and Larry Hendrickson* (SD), determined by G. A. Levin, confirmed by D. J. Keil.

Previous knowledge. Previously known from the Cascade/Sierra Nevada axis north to southern OR and in the North Coast Ranges from Lake Co. to Trinity Co.

Significance. A range extension of ca. 300 km SE from Kern Co., CA. First record for any member of *Helianthella* south of the central Coast Ranges or the southern Sierra Nevada.

—MICHAEL CURTO and LINDA ALLEN, Robert F. Hoover Herbarium, California Polytechnic State University, San Luis Obispo, CA 93407; GEOFFREY A. LEVIN,

Botany Department, San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112; and LARRY HENDRICKSON, P.O. Box 155, Julian, CA 92036.

VIOLA LANGSDORFII (Regel) Fisch. (VIOLACEAE).—Del Norte Co., NW side of Lake Earl, W of Fort Dick, in bogs among coastal sand dunes, with *Helenium bolanderi, Gentiana sceptrum, Botrychium multifidum,* T17N, R1W, sect. 20, 12 May 1992, *Hammond s.n.* (CAS, NY, OSC, UC).

Previous knowledge. NE Asia to Alaska and W. British Columbia. It was collected once in Oregon (Curry Co., Brookings, 29 June 1938, *M. S. Baker 9060,* holotype of *V. superba* M. S. Baker, Madroño 5:220–223. 1940; UC, isotype WILLU), but has not been seen in recent years.

Significance. First record for California. Reported by Jepson (Manual of the Flowering Plants of California, 647, 1925) but withdrawn (op. cit., 1170) as being confused with *V. palustris* L. Distinguished from *V. palustris* by larger flowers (width of dorsal petals 7–11 mm vs. 4–6 mm), presence of leafy flowering stems (vs. flowers arising from rhizome), and absence of filamentous stolons (present in *V. palustris*).

—PAUL C. HAMMOND, Department of Entomology and KENTON L. CHAMBERS, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331.

IDAHO

ASCLEPIAS INCARNATA L. (ASCLEPIADACEAE).—Canyon Co., Notus, 27 Aug 1986, *R. Old s.n.* (ID, WS).

Previous knowledge. Manitoba and New Mexico to Florida and Maine (Barkley, Flora of the Great Plains, 1986).

Significance. First report from the Pacific Northwest. Not included in the Flora of the Pacific Northwest (Hitchcock & Cronquist 1973) or the Flora of Idaho (Davis 1952).

—RICHARD R. OLD, P.O. Box 272, Pullman, WA 99163; JOSEPH E. LAFERRIÈRE, see below, and JOY D. MASTROGIUSEPPE, Marion Ownbey Herbarium, Washington State University, Pullman, WA 99164-4309.

EUPHORBIA DENTATA Michx. (EUPHORBIACEAE).—Idaho Co., 10 km N of Lucille along Salmon River, just S of highway department maintenance building along roadside, 22 Sep 1986, *R. Old s.n.* (ID, WS).

Previous knowledge. NY, MN, SD, WY, UT, S to VA, LA, TX, AZ and Mexico (Fernald, Gray's manual of botany, 8th ed., 1970; Barkley, Flora of the Great Plains, 1986).

Significance. First report from Idaho. The current report probably represents a recent introduction rather than an extension of the natural range of the species. The plant is a frequent weed along roadsides and other waste areas in its previously known range.

—RICHARD R. OLD, P.O. Box 272, Pullman, WA 99163; JOY D. MASTROGIUSEPPE, Marion Ownbey Herbarium, Washington State University, Pullman, WA 99164-4309, and JOSEPH E. LAFERRIÈRE, see below.

VERBASCUM VIRGATUM Stokes (SCROPHULARIACEAE).—Bannock Co., Milepost 61 southeast of Pocatello, 23 Aug 1986, *Old s.n.* (ID).

Previous knowledge. Native to Europe, naturalized in eastern and southern North America from Nova Scotia and Ontario south to South Carolina, Texas, and southern California (Fernald, Gray's manual of botany: eighth (centennial) edition, 1970; Munz, A California flora with supplement, 1968).

Significance. First report from the Pacific Northwest.

—RICHARD R. OLD, P.O. Box 272, Pullman, WA 99163; JOSEPH E. LAFERRIÈRE, see below, and JOY D. MASTROGIUSEPPE, Marion Ownbey Herbarium, Washington State University, Pullman, WA 99164-4309.

IDAHO, OREGON and WASHINGTON

CHAENORRHINUM MINUS (L.) Lange in Wilk. & Lange (SCROPHULARIACEAE).—IDAHO. Idaho Co., Cottonwood, Sep 1987, *F. E. Northam 87-7* (IDW*). Nez Perce Co., along Lapwai Creek south of Culdesac, 15 Sep 1986, *R. Old s.n.* (ID, IDW). OREGON. Union Co., Imbler, 19 Aug 1987, *Gladys Anderson s.n.* (ORE, OSU). WASHINGTON. Spokane Co., shoulder of Interstate 90 just west of Idaho/Washington state line truck scales, 14 Sep 1986, *R. Old s.n.* (ID, WS); shoulder of Highway 195 ¼ mi north of Spangle turnoff, 11 Sep 1990, *R. S. Nielsen s.n.* (WS); Spangle, along sides of Highway 395, 15 Jul 1991, *C. Roché 1492* (WS). Whitman Co., gravel parking area northeast of Pullman, 20 Dec 1991, *R. Old & J. Mastrogiuseppe 6984* (WS); Snake River downstream from Steptoe Canyon at Railroad Milepost 54, 10 Nov 1989, *R. Old s.n.* (IDW). [* IDW = Plant Materials Collection, Department of Plant, Soil, and Entomological Sciences, University of Idaho.]

Previous knowledge. A native of southern Europe, the species is naturalized in eastern North America from eastern North Dakota and Kansas to Virginia and Nova Scotia (Fernald, Gray's manual of botany, 8th edition, 1970; Barkely, Flora of the Great Plains, 1986). It has also been reported from clearings and roadsides in Douglas fir forests in British Columbia (Taylor & MacBryde, Vascular plants of British Columbia: a descriptive resource inventory, 1977).

Significance. First reports for Idaho and Washington. Not listed in the Flora of the Pacific Northwest (Hitchcock & Cronquist 1973). Recently classified as a Class A noxious weed in Washington (Roché, PNW Extension Bulletin 378, 1991).

—RICHARD R. OLD, P.O. Box 272, Pullman, WA 99163; CINDY T. ROCHÉ, Department of Natural Resource Sciences, Washington State University, Pullman, WA 99164-6410; JOY D. MASTROGIUSEPPE and JOSEPH E. LAFERRIÈRE, see below.

NEW MEXICO

PANICUM MOHAVENSE J. Reeder (POACEAE).—Socorro Co., White Sands Missile Range, Oscura Mts., 49 air km ESE of San Antonio, extreme W edge of North Oscura Peak, T6S R5E sect. 25 (SW corner), on thin limestone soil trapped in flat pockets at extreme cliff edge, with *Juniperus monosperma, Pinus edulis, Thelesperma, Bouteloua,* elev. 2380 m, 26 Aug 1988, *Spellenberg & Brozka 9682* (ARIZ, NMC). Only three plants were found in extensive searching of cliff edge; no plants were located at the same site in September 1990. Plants did not occur in the more mesic microsites away from the cliff edge.

Previous knowledge. This recently described species (1991. Phytologia 71:300–303) was known from only the Main Street Valley area of Mohave Co., northwestern Arizona, on limestone.

Significance. First record NM, a second site for the species, representing a ca. 700 km southeastward range extension, and an upward elevational range extension of ca. 800 m (identification confirmed by J. Reeder). The species is one of several (*Salvia davidsonii* [following], *Apacheria chiricahuensis* [Madroño 38:298]) that are much more western that have the easternmost known limits in these mountains or the San Andres Mts. to the immediate south.

SALVIA DAVIDSONII Greenm. (LAMIACEAE).—Doña Ana Co., S end of San Andres Mts. in Ash Canyon, 44 air km NE of Las Cruces, T12S R4E sect. 21 (SW corner), elev. 1615 m, 21 Jul 1988, *P. Hoban 152* (NMC); Sierra Co., White Sands Missile Range, San Andres Mts., Bear Den Canyon, 4 km from Rhodes Canyon, elev. 1810–2010 m, 28 Aug 1991, *Anderson & Morrow 5085* (NMC); Socorro Co., W base of Oscura Mts., 53 air km SE of San Antonio, 5 km E of Miller's watch, elev. 2035 m, 3 Sep 1990, *Spellenberg, Brozka, & Hoban 10603* (MO, NMC, NY, UC, UNM), 2070 m, 19 Aug 1991, *Spellenberg & Anderson 10865* (ID, MO, NMC, NY, RSA, TEX, UC, UNM); N end of Oscura Mts., in North Canyon, elev. 1845 m (several collections in this canyon, which is about 3 km long), 7 Aug 1991, *Anderson 4946* (NMC), 14 Aug 1991, *Anderson 4979*, 19 Aug 1991, *Spellenberg & Anderson 10866* (ARIZ, NMC, NY), *Spellenberg & Anderson 10867* (NMC), 24 Apr 1992, *Spellenberg & Zucker 10991* (NMC; an April 1992 garden collection from Las Cruces from plants collected at the #10865 site 31 Aug 1991).

Previous knowledge. Known only from north-central to southeastern Arizona according to search of specimens by R. Van Devender (ARIZ) and L. Landrum (ASU).

Significance. The exact nature of *S. davidsonii* is not clear, as discussed below, and identification of these collections must remain tentative, the problem as to why explained here. As identified, this is the first report for this species for NM, a range extension eastward of at least 290 km. Our specimens match well specimens from Arizona seen by Greenman at MO, and key readily to the species in the Arizona Flora (Kearney and Peebles 1960) by corolla length and by leaf characteristics. Specimens identified as *S. davidsonii* filed in Arizona herbaria were reported by curators to have corolla lengths of 1.7–4 cm, the color described on specimen labels as pinkish-lavender to red. In the original description (1905, Proc. Amer. Acad. Arts and Sci. 41:246) Greenman described the corolla as about 1 cm long, red. All the field-collected material from New Mexico has corollas much shorter than the calyx, the longest at 13 mm and barely protruding from the tube, others barely or not protruding from the tube and about 5–8 mm long and bright, deep pink. The limb of most of these did not open; a few opened very slightly, but it is doubtful that pollen transfer between such flowers would be common. Dissection of these corollas indicated that anthers had burst, and fruit set was good on older flowers. These plants approach or achieve cleistogamy, a condition apparently not reported for Southwestern species (nor have we seen references to this condition in the genus). Early in the season, however, plants may be widely chasmogamous in the field (we could not revisit these remote sites). Collection *10911,* cited above, comes from plants from population *10865.* These were cleistogamous in August of the previous year in the field, but in the garden in Las Cruces, in April 1992 they had brilliant deep pink chasmogamous corollas 22–28 mm long. Unfortunately, plants did not survive the spring burst of growth and it is unknown if a late season change to cleistogamy would occur in the garden situation.

A review of specimens at TEX indicate that our plants could as easily be a form of *S. roemeriana* Scheele, a species with corollas 25–35 mm long and which like *S. davidsonii* often has leaves simple by reduction but that are wider. *Salvia roemeriana* is also unknown in New Mexico. It is very closely related to *S. henryi,* a species that more consistently has divided leaves and reputedly differs in the quality of corolla corolla (deep scarlet in *S. roemeriana* vs. red). If leaves are simple by reduction in *S. henryi,* the remaining lobe is said to be deeply cleft or angulately lobed (corolla color and leaf characteristics from D. S. Correll and M. C. Johnston, 1970, Manual of the Vascular Plants of Texas). One such collection identified as *S. henryi* is that

of *Worthington, s.n.,* 6 Dec 1977, Texas, El Paso Co., Tom Mays Park (TEX), where the collector notes flowers apparently were pink when fresh. This specimen has shallowly lobed, simple leaves and is indistinguishable from our collections identified as *S. davidsonii* above. A collection seen at MO (*U. T. Waterfall 5375,* Texas, Hudspeth Co., Sierra Diablo, about 20 miles north of Allamore, limestone cliffs and ledges along bottom of Victoria Canyon near its upper end; with *Juniperus, Pinus* and *Fraxinus cuspidata,* 28 July 1943) was identified as *S. davidsonii* by the collector. It is very similar in form to our plants, and its habitat is very similar to that from which our collections originate. Apparently this collection was not seen in the preparation of *Salvia* for the Manual of Vascular Plants of Texas. This trio of named entities is in need of careful field and garden study.

—RICHARD SPELLENBERG, Biology Department, New Mexico State University, Las Cruces, NM 88003-0001; DAVID ANDERSON, Environmental Services Division, STEWS-ES-E, White Sands Missile Range, NM 88002-5076; and ROBERT BROZKA, Const. Eng. Lab., US Army Corp Engineers, P.O. Box 9005, Champaign, IL 61826-9005.

WASHINGTON

PLATANTHERA ORBICULATA (Pursh) Lindley var. *ORBICULATA* (ORCHIDACEAE).—Stevens Co. 3 km SW of Spirit, T38N, R41E, sect. 7 NE¼ of NE¼, on NW-sloping ridge in a nearly pure stand of *Larix occidentalis* Nutt., elev. approx. 2800 feet (840 m), 9 Jun 1992, *J. E. Laferrière & P. S. Gallo 2610* (WS). This is a photospecimen because of the extremely small population size (only two individuals were observed).

Previous knowledge. Southeastern tip of AK to Newfoundland, along the mountains S to northern OR in the W and NC in the E (C. A. Luer, The native orchids of the United States and Canada excluding Florida, New York Botanical Garden, New York, 1975); Pend'Oreille, San Juan, Snohomish, Spokane, and Whatcom counties, Washington (Washington State Natural Heritage Program, An illustrated guide to the endangered, threatened and sensitive vascular plants of Washington, Department of Natural Resources, Olympia, 1981).

Significance. First report from Stevens Co. The species is listed as monitored (Washington State Natural Heritage Program, Endangered threatened & sensitive vascular plants of Washington, Department of Natural Resources, Olympia, 1990).

—PATTI S. GALLO, P.O. Box 669, Troy, ID 83871-0669; and JOSEPH E. LAFERRIÈRE, Arnold Arboretum, Harvard University, Cambridge, MA 02138.

ERRATUM

In "New chromosome counts in Madiinae (Asteraceae) and their systematic significance" by Bruce G. Baldwin (Madroño 39(4):308, 1992), the last sentence of the next to last paragraph should read: "Morphologically, they are distinguished from other annual *Madia* species by their *combination of* yellow anthers and pappose disk flowers."

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Contents

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ROLE OF HIGH FIRE FREQUENCY IN DESTRUCTION OF MIXED CHAPARRAL

Tori L. Haidinger and Jon E. Keeley*
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Abstract

Postfire regeneration of *Adenostoma* and *Salvia* dominated chaparral was studied in adjacent sites burned by wildfire once, twice, or three times in the past six years, at intervals of 1, 4, and 6 yr prior to the study. The following combinations of burning were: 1 yr ago (previous burn was >20 yr); 1 and 6 yr ago; 1, 4, and 6 yr ago; 4 and 6 yr ago; and 6 yr ago. Marked changes in community composition occurred as fire frequency increased. On the site that burned only once in the past several decades the dominant shrubs *Adenostoma fasciculatum* and *Salvia mellifera* established abundant seedling populations in the first growing season after fire. Seedling establishment the first season after fire was 62% (*S. mellifera*) to 83% (*A. fasciculatum*) less on the site that had also burned 6 yr previously and zero on the site that had burned 1, 4, and 6 yr ago. The suffrutescent (chamaephyte) *Lotus scoparius,* likewise showed the lowest seedling establishment on the site burned the most frequently, however, it did best on the site burned 1 and 6 yr ago. Although *Adenostoma fasciculatum* resprouts after fire, there was some mortality after each fire and thus the number of resprouting shrubs diminished as fire frequency increased. Postfire annual species, in general, were abundant on all sites burned 1 yr ago, regardless of the prior fire frequency. Non-native species such as *Brassica nigra, Bromus* spp., and *Schismus barbatus* were poorly represented on the 1 yr old burn that had not been repeatedly burned in recent years. In general, as fire frequency increased, these non-native weeds increased dramatically. It is suggested that high fire frequency has played an important role in the establishment of these weeds and conversion from shrub-dominated to herbaceous-dominated ecosystems in the California landscape.

California chaparral is a "fire-type" vegetation that not only regenerates rapidly after wildfires, but many species are dependent upon such disturbance for regeneration (Horton and Kraebel 1955; Hanes 1971; Keeley and Keeley 1988). It seems reasonable, however, that different fire regimes may generate different patterns of postfire community composition, due largely to the fact that different regimes favor different plant species.

Gill (1973) distinguished three components of fire regime: fire frequency, fire intensity, and fire season. Fire frequency plays a dominant role in determining vegetation structure and vegetation structure largely determines fire intensity. In California chaparral, Zedler et al. (1983) described the impact of two fires only a year apart, on postfire regeneration of the woody vegetation at several mixed chaparral sites. The effect of this extreme event was to nearly eliminate

one obligate-seeding *Ceanothus* species and greatly reduce the abundance of *Adenostoma fasciculatum*. Thus, it was shown that these two "fire-type" shrubs, which require fire for seedling recruitment, are negatively impacted by frequent fires.

The present study examines the impact of multiple fires on postfire regeneration of mixed "hard" and "soft" chaparral dominated by *Adenostoma fasciculatum* and *Salvia mellifera* in southern California. Here we extend the studies of Zedler et al. (1983) and others by following the concomitant changes in both woody and herbaceous elements. Our study takes advantage of a unique natural experiment in which adjacent sites were burned by wildfires at different intervals in the past 6 yr.

Study Sites and Methods

The study sites were on the north side of the Verdugo Mountains, which are considered to be an extension of the San Gabriel Mountain Range. The sites were west of Sheep Corral Canyon, T2N R13W sect. 30, 600 m elevation. The study was carried out in spring 1992 and sampling was done on adjacent sites burned at different intervals over the past 6 yr as described below. The precipitation records for the nearest station La Crescenta (5 km east and 125 m lower) for this period were: 1986–1987 = 292 mm, 1987–1988 = 556 mm, 1988–1989 = 583 mm, 1989–1990 = 338 mm, 1990–1991 = 545 mm, 1991–1992 = 894 mm (44 yr average = 586 mm) (NOAA 1986–1992).

A large portion of this area burned in 1986 (Keeley unpublished data). In 1988 approximately half of the 1986 burn-site burned again, and in 1991 approximately half of the 1988 burn-site burned a third time. Thus, the following combinations of burning frequency at the time of the study in spring 1992 were: 1 yr ago; 1 and 6 yr ago; 1, 4, and 6 yr ago; 4 and 6 yr ago; and 6 yr ago. Based on the size of *Adenostoma fasciculatum* shrubs in the portions of the site missed by all recent fires it appeared that the shrubs were >20 yr of age at the time of the 1986 burn.

Sites were sampled by random placement of 10 4-m-square quadrats within each site and recording the number of all shrub seedlings and resprouts. Nested within each quadrat a 1-m-square plot was sampled for herbaceous species. Sites were compared statistically with a one-way ANOVA and Duncan's multiple range test. Nomenclature follows Munz (1974).

Results

The dominant hard-chaparral shrub at the site, *Adenostoma fasciculatum,* re-established after fire from both resprouts and seedlings (Figs. 1 and 2). On the one yr site that burned only once in 6 yrs,

A. fasciculatum seedling density was 7.1 times greater than the pre-fire population size (based on total number of resprouting shrubs and dead shrub skeletons). Seedling establishment by *A. fasciculatum* was markedly reduced on sites that had burned more than once in the past 6 yr (Fig. 2) and this pattern was also seen for the dominant soft-chaparral shrub *Salvia mellifera* (Fig. 3). The suffrutescent *Lotus scoparius* likewise showed the lowest seedling establishment on the site burned the most frequently, however, it did best on the site burned 1 and 6 yr ago (Fig. 4). *Marah macrocarpus* is a resprouting herbaceous vine that was also absent on the most frequently burned site (Fig. 5) as was the native annual *Cryptantha* sp. (Fig. 6).

Postfire native annual species, which are typical of postfire burned sites, were abundant on all sites burned 1 yr ago, regardless of the prior fire frequency (Figs. 7–9).

Non-native species such as *Brassica nigra, Bromus* spp., and *Schismus barbatus* were absent or poorly represented on the 1 yr old burn that had last burned more than 20 yr ago (Figs. 10–12). However, postfire recruitment of these aliens was substantially increased on sites that were repeatedly burned. *Brassica nigra* and *Bromus* spp. were particularly abundant on the most frequently burned site.

The composition of the community changed with increasing fire frequency. In general, as the number of fires increased the percentage of annuals increased (Fig. 13) and the percentage of non-native exotics increased (Fig. 14). Species richness was greatest on the site burned 1 and 6 yr ago (16 species) and lowest on the site burned 1, 4, and 6 yr ago (10 species).

Discussion

This study attempts to take advantage of a natural experiment that is not readily duplicated under controlled conditions. Of course the inherent weakness of utilizing such natural experiments is lack of replication. Therefore, it is prudent to clarify that conclusions about the role of fire frequency lack replication and we can not put statistical bounds around the possibility that observed patterns reflect site-to-site variability rather than reponses to fire frequency.

The results of this study, however, are consistent with the observation that fire-adapted chaparral species are not adapted to all fire regimes. As Zedler et al. (1983) noted, high fire frequency may have devastating impacts on shrub species that require a period of recovery before being resilient to further disturbance. At our sites, *Adenostoma fasciculatum* re-established well from both seedlings and resprouts after a single fire. This species requires a period of time after fire for development of a seed bank sufficient to insure adequate seedling recruitment after a repeat fire (Fig. 2). Addition-

1. Adenostoma Repsrouts

2. Adenostoma Seedlings

3. Salvia mellifera

4. Lotus scoparius

5. Marah macrocarpa

6. Cryptantha sp.
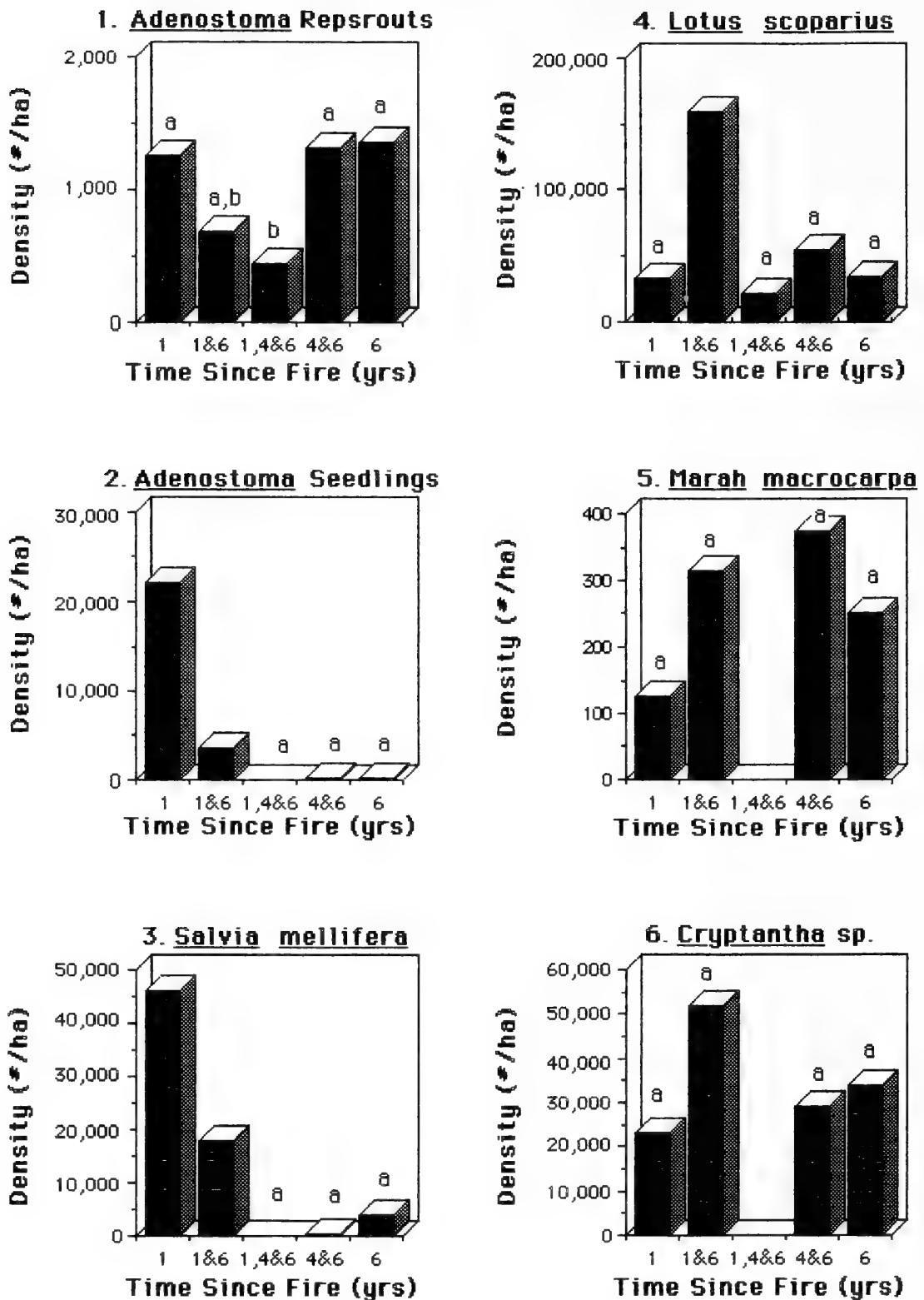
Figs. 1–12. Density of dominant species in the five study sites. Bars capped with the same letter are not significantly different at P < 0.05, n = 10.

ally, although this shrub is a resprouter, it is not immune to fires and there is significant attrition with each repeat fire (Fig. 1).

Others, such as the soft-chaparral/coastal sage shrub *Salvia mellifera,* follow a similar pattern (Fig. 3), in that repeat fires are destructive to their persistence on a site. The rapidly growing suffru-

7. Phacelia grandiflora

10. Brassica nigra

8. Eucrypta chrysanthemifolia

11. Bromus spp

9. Camissonia bistorta

12. Schismis barbatus
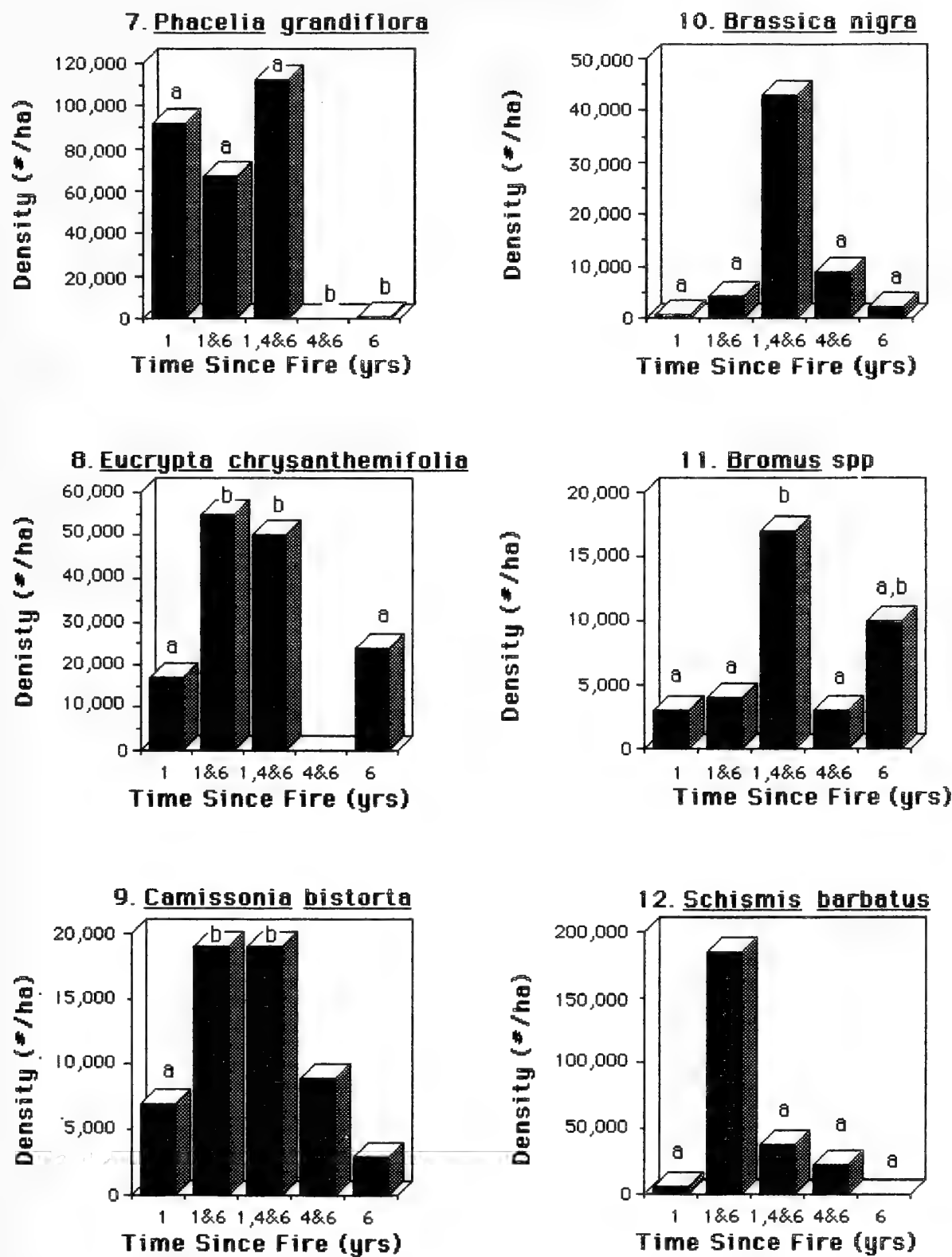
FIGS. 1–12. Continued.

tescent, *Lotus scoparius,* although negatively affected by three fires in 6 yr, seems well adapted to fires at 5 yr intervals (Fig. 4). This suffrutescent is relatively short-lived and is a temporary postfire species. Apparently it is capable of developing sufficient seed banks during shorter fire-return intervals than other chaparral perennials.

13. Annuals and Perennials

14. Natives and Exotics
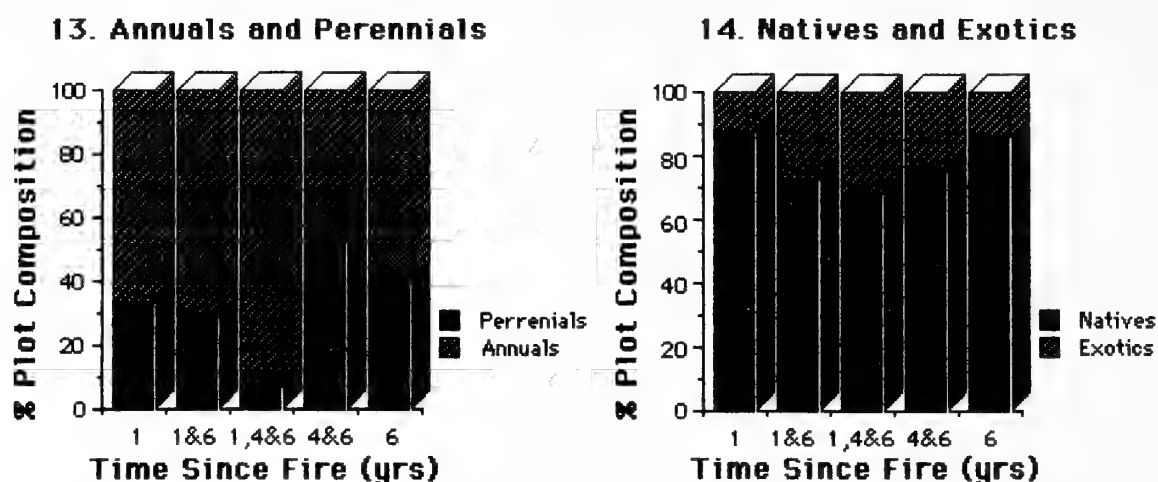
FIG. 13. Percentage of annuals and perennials in the five study sites. FIG. 14. Percentage of natives and exotics in the five study sites.

However, even this species has its limits and fares poorly when the fire frequency exceeds three times in 6 yr.

In general, annuals are well adapted to frequent fires. Natives and non-natives are separable in one important respect. The recent burn that occurred on a site not previously burned in several decades was dominated by natives such as *Phacelia grandiflora* and *Eucrypta chrysanthemifolia* (Figs. 7 and 8). In contrast, non-native annuals such as *Brassica nigra* and species of *Bromus* were poorly represented and were abundant only after the area burned repeatedly (Figs. 10–12).

The present study illustrates the potential role of high fire frequency in altering the California landscape from a shrub dominated ecosystem to an herbaceous dominated system. The apparent permanence of such changes is attested to by numerous studies that reveal the limited ability of coastal sage and chaparral shrubs to (re)invade sites dominated by non-native annual grasses and forbs (White 1966; Freudenberger et al. 1987; Hobbs 1983; Davis and Mooney 1985). Part of the explanation lies in the changes in soil water availability produced by the annual flora. Loss of native nitrogen-fixing species such as *Lotus scoparius* and *Ceanothus* spp. may result in additional changes in ecosystem properties that further limit the ability of shrubs to re-establish on these annual-dominated sites.

While it should not be surprising that repeated disturbance enhances the spread of non-natives, these results do call into question the conclusions of Westman (1979) that oxidant levels enhance the spread of non-natives. In Westman's study it was shown that levels of particular air pollutants were correlated with the percentage of non-natives (mostly annuals) in coastal sage scrub vegetation. Unfortunately, Westman (1979) did not investigate the correlation between fire frequency and non-native abundance. Although Westman (1979) appreciated the role of fire in structuring of coastal sage com-

munities, he lacked data on the frequency of fires at his sites. In his attempt to correlate the abundance of non-natives with site factors, he utilized the time-since-last-fire as a measure of fire history and sampled only sites that had not burned in 7 yr. Based on Westman's criteria, after 6 yr, all sites from the present study would be scored as having experienced the same fire history. It is little wonder that Westman (1979) found no correlation between non-native abundance and his surrogate measure of fire history. Westman's correlation between non-natives and air pollution may be spurious since oxidant levels are likely to be highly correlated with fire frequency. In other words, fire frequency, as well as oxidant level, increases in urban environments (Keeley 1982), and thus the correlation between oxidant level and non-natives should not necessarily be interpreted as representing a causative relationship.

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ALLOZYME DIFFERENTIATION AMONG *BEALIA MEXICANA, MUHLENBERGIA ARGENTEA,* AND *M. LUCIDA* (POACEAE: ERAGROSTIDEAE)

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Abstract

Allozyme data were used to evaluate the genetic variation, relationships, and population genetic structure of three endemic grasses: *Bealia mexicana, Muhlenbergia argentea,* and *M. lucida.* Electrophoretic examination of 20 putative enzyme loci in 14 populations revealed that all three species have high genetic variability (H ranging from 0.19 to 0.26; F ranging from 0.073 to -1.000) indicative of mixed mating and outcrossing plants, this variation being sequestered within populations in *B. mexicana* and *M. lucida* and among populations in *M. argentea.* The highest allozymic similarity occurred between *B. mexicana* and *M. argentea* (I = 0.83) rather than between *M. lucida* and *M.argentea* (I = 0.59). At present, populations of the geographically restricted *B. mexicana* and *M. argentea* are not threatened due to lack of genetic variation and their survival depends on the maintenance of critical habitat.

Resumen

Mediante el análisis de alozimas se evaluó la variación genética, relaciones y estructura genético de tres gramíneas endémicas: *Bealia mexicana, Muhlenbergia argentea* y *M. lucida.* El examen electroforético de 20 loci putativo enzimaticos en 14 poblaciones reveló que las tres especies tienen una alta variabilidad genética (H varía de 0.19 a 0.26; F varía de 0.073 a -1.000), indicadora de aparejamiento variado y polinización cruzada, estando esta variación dividida dentro de las poblaciones en *B. mexicana* and *M. lucida* y entre poblaciones en *M. argentea.* Se encontró mayor similitud alozimica entre *B. mexicana* y *M. argentea* (I = 0.83) que entre *M. lucida* y *M. argentea* (I = 0.59). Actualmente poblaciones de las geograficamente restringidas *B. mexicana* y *M. argentea* no se encuentran en amenaza debido a falta de variación genética y su supervivencia depende de que se mantenga su hábitat crítico.

Muhlenbergia Schreb. is a large, primarily New World genus of perhaps 160 species, most of which occur in the arid lands of the southwestern United States and north-central Mexico. The genus, as now interpreted, is morphologically very diverse and probably represents a taxonomic dumping ground (Correll and Johnston 1970;

Peterson and Annable 1991; Peterson et al. 1989). The revision of the entire genus is currently underway and will undoubtedly result in additional re-alignment of some species as has already been accomplished for some taxa (Peterson 1989; Peterson and Annable 1990, 1991, 1992; Peterson unpublished data).

Bealia mexicana Scribn. in Beal, *Muhlenbergia argentea* Vasey, and *M. lucida* Swallen are morphologically very similar and have been suggested by various authors as being closely related (Hitchcock 1935; Swallen 1936; Peterson 1989). They all possess an unusual feature, the occurrence of a deeply bilobed lemma with a crisped-curled to flexuous awn borne between the two lobes (Peterson 1989). However, the lobe apices in *B. mexicana* and *M. argentea* are obtuse to rounded and in *M. lucida* the apices are acute. *Muhlenbergia lucida* also has tightly involute leaf blades whereas *B. mexicana* and *M. argentea* have flat to very loosely involute leaf blades.

Muhlenbergia argentea and *M. lucida* are caespitose perennials from the Sierra Madre Occidental of western Chihuahua, Mexico. *Muhlenbergia argentea* is restricted in range and habitat and occurs on reddish rhyolitic lava flows in seasonally wet rocky crevices usually associated with a cliff face, at elevations between 1780–2100 m. It is known from only three localities, one just above the Cascada de Basaseachic and the other two northeast of La Bufa on the cliffs above the Rio Batópilas. *Muhlenbergia lucida* is more wide ranging in the Sierra, where it occurs on gray to reddish or white volcanic pumice, lapilli tuff and altered rhyolite lava flows in dry rocky sites among boulders at elevations between 2000–2600 m.

Bealia Scribn. in Hack. is a monotypic genus known from only a few localities in the Sierra Madre Occidental in Chihuahua and Durango, Mexico. Until only recently, *Bealia mexicana* was placed in *Muhlenbergia* (*M. biloba* Hitchc.), but with new cytological and existing morphological evidence this species has been reinstated in its own genus (Peterson 1989). *Bealia mexicana* can be differentiated from *Muhlenbergia* by possessing deeply bilobed lemmas (1–1.4 mm long) with rounded to obtuse lobes, crisped-curled to flexuous awns born between the lobes, minutely glandular pedicels, loosely pilose to villous, single-nerved glumes, and by its annual life form. In *Muhlenbergia* the lemma is usually not deeply bilobed, although the apex can sometimes be emarginate to shallowly lobed with acuminate to aristate teeth less than 1 mm long (*M. argentea* is the exception), the awns are usually straight to flexuous (*M. argentea, M. crispiseta* Hitchc. and *M. flaviseta* Scribn. have crisped-curled awns), the pedicels are eglandular, and both perennials and annuals are common. *Bealia mexicana* is presently known from only four localities in the Sierra and is restricted to whitish, shallow and sandy, volcanic, lapilli tuff soils on flat escarpments or ledges at elevations between 2000–2300 m.

In *Muhlenbergia* and other Eragrostideae the base chromosome number is generally 10 and only *Bealia, Blepharoneuron* Nash, *Chaboissaea* Fourn., *Crypsis* Ait., *Dasyochloa* Willd. ex Rydb., *Erioneuron* Nash, and *Munroa* Torr. have a base number of 8 (Gould 1958; Hammel and Reeder 1979; Peterson 1988, 1989; Peterson and Annable 1990, 1992; Reeder 1967, 1968, 1971, 1977; Reeder and Reeder 1988; Tateoka 1961). Cladistic analysis of chloroplast DNA restriction fragment variation suggests a close relationship among *Bealia, Blepharoneuron, Chaboissaea,* and *Muhlenbergia,* excluding *Dasyochloa, Erioneuron,* and *Munroa* (Duvall et al. in review). *Crypsis,* although morphologically similar to *Muhlenbergia,* is probably more closely allied with *Sporobolus* where it shares 1-nerved lemmas, caryopses with free pericarps, and hairy ligules.

The present study was initiated to estimate the genetic differentiation within and among populations of *B. mexicana, M. argentea,* and *M. lucida.* We also wanted to determine whether allozymic data could clarify relationships and allow the evaluation of the population genetic structure between the annual and perennial life form in highly endemic species. There is very little information describing the genetic diversity of geographically restricted, potentially endangered grasses. This study is the first population-based analysis of soluble enzymes in *Muhlenbergia* and *Bealia,* a related genus.

MATERIAL AND METHODS

One hundred individuals from four populations of *B. mexicana,* 78 individuals from three populations of *M. argentea,* and 178 individuals from seven populations of *M. lucida* were examined for electrophoretic variation (Table 1). Fresh leaf blades or entire plants, if a small annual, were collected in the field, placed in a 3.6 ml Nunc cryotube, and frozen on site in liquid nitrogen.

Floral buds were field collected and fixed in ethanol–acetic acid (3:1, V:V) prior to storage under refrigeration in 70% ethanol. Meiotic chromosome counts were obtained from aceto-carmine squashes on pollen mother cells. Representative cells were recorded with sketches and photographed using Kodak Technical Pan film. Chromosome number determinations were based on observations of 10 or more cells at diakinesis.

Sample preparation and electrophoresis of enzymes followed the general methodology of Morden et al. (1987). Approximately 300 mg of mature tissue from each plant was homogenized in up to 25 drops of grinding buffer (Morden et al. 1987) together with about 50 mg of sea sand to enhance disruption of cells. Extracts were absorbed into 2 × 11 mm Whatman filter paper wicks and stored at −80°C. Electrophoresis was conducted in the four gel/buffer systems of Morden et al. (1987): L, M, N, and T, however, starch content

TABLE 1. FIELD COLLECTIONS OF *BEALIA MEXICANA, MUHLENBERGIA ARGENTEA, M. LUCIDA, CHABOISSAEA DECUMBENS, C. LIGULATA*, AND *C. SUBBIFLORA* ANALYZED BY ENZYME ELECTROPHORESIS. Chromosome numbers are given in parenthesis. Voucher specimens are deposited at US.

B. mexicana. MEXICO. **Chihuahua:** Parque Natural Cumbres de Majalca, Colonia Cumbres de Majalca, *Peterson, Annable & Herrera 7946*; Parque Natural Cumbres de Majalca, W of Cumbres de Majalca, *Peterson, Annable & Herrera 7981* (n=16); S of Villa Matamoros, *Peterson & King 8264* (n=16). **Durango:** SW of El Ojito, *Peterson, Annable & Herrera 8090.*

M. argentea. MEXICO. **Chihuahua:** Parque Natural Barranca del Cobre, NE of La Bufa, *Peterson, Annable & Herrera 8044, 8066* (n=10); Cascada de Basaseachic, *Peterson & King 8248.*

M. lucida. MEXICO. **Chihuahua:** Parque Natural Cumbres de Majalca, Colonia Cumbres de Majalca, *Peterson, Annable & Herrera 7973*; Parque Natural Cumbres de Majalca, W of Cumbres de Majalca, *Peterson, Annable & Herrera 7978*; Parque Natural Barranca del Cobre, S of Creel, *Peterson, Annable & Herrera 8029*; Parque Natural Barranca del Cobre, NE of Batópilas, *Peterson, Annable & Herrera 8039*; E of Guachochi, *Peterson, Annable & Herrera 8083*; W of La Junta, *Peterson & King 8202*; Parque Natural Cumbres de Majalca, Cascada de Basaseachic, *Peterson & King 8249.*

C. decumbens. MEXICO. **Chihuahua:** W of Cuauhtemoc, *Peterson, Annable & Herrera 7983.*

C. ligulata. MEXICO. **Chihuahua:** N of Cuauhtemoc, *Peterson & Annable 8111.*

C. subbiflora. MEXICO. **Durango:** N of Durango, *Peterson & King 8266.*

was modified to optimize gel handling characteristics and improve resolution. All gels consisted of a 2.6:1, Electrostarch : Sigma Starch ratio with a total starch content of 13.5%, 11.5%, 11.5%, and 13.0% for the L, M, N, and T systems, respectively. For each population, samples from all individuals were included together on the same gel. Selected individuals from different populations were then analyzed together for purposes of interspecific and interpopulational caparisons. Gels were sliced and stained for the following 14 enzymes: aspartate aminotransferase (AAT), aconitase (ACO), adenylate kinase (ADK), aminopeptidase (AMP), fructokinase (FRK), glutamate dehydrogenase (GDH), glutamate-pyruvate transaminase (GPT), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (PGD), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), shikimate dehydrogenase (SAD), and triose phosphate isomerase (TPI). Only the plastid form of IDH was surveyed. Loci were designated sequentially with the most anodally-migrating isozyme designated 1, the next 2, and so on. Alleles were designated sequentially with the most anodally migrating allele given an *a,* the next *b,* and so on.

Values for Nei's (1972) genetic identity (I) and distance measures were computed for pairwise comparisons using BIOSYS-1 (Swofford and Selander 1989). Standard measures of genetic variation (Table 3) were computed for *B. mexicana, M. argentea,* and *M. lucida,*

including mean number of alleles per locus (A), proportion of polymorphic loci (P), mean heterozygosity (H), and mean fixation (F) index which measures the deviation of genotypic proportions from Hardy-Weinberg expectations (Jain and Workman 1967; Swofford and Selander 1989). The distribution of genetic variation within the three taxa was determined using F-statistics (Table 4) where F_{IS} is the fixation index within populations, F_{IT} is the overall fixation index, and F_{ST} measures the amount of differentiation among populations (Wright 1965, 1969). The patristic distance matrix was calculated using the Prevosti distance index (Wright 1978) and after optimization of branch lengths a corresponding Wagner tree (Fig. 1) was produced using *Chaboissaea decumbens* (Swallen) J. & C. Reeder, *C. ligulata* Fourn., and *C. subbiflora* (Hitchc.) J. & C. Reeder as outgroups (Swofford and Selander 1989).

RESULTS

New chromosome counts (Table 1) were made in three populations: two of *B. mexicana* ($n=16$) and one of *M. argentea* ($n=10$). A previous reported chromosome count for *B. mexicana* from the same locality as population *8090* indicated a diploid at $n=8$ (Peterson 1988). The earlier count is probably in error since no irregularities in the meiotic chromosome pairing, such as univalents or trivalents, were noted in the new preparations of *B. mexicana*. Therefore, all populations analyzed in this study were interpreted to be diploid. However, *B. mexicana* could still be an autopolyploid or an allopolyploid with some duplicated loci expressed and some silenced.

Twelve enzymes with 20 putative loci were consistently scorable by starch gel electrophoresis: AAT-1, AAT-2, AAT-3, ACO-1, ACO-2, AMP-2, GDH, GPT-1, GPT-2, IDH-1, MDH-1, MDH-2, MDH-3, PGD-1, PGD-2, PGI-1, PGI-2, PGM-1, SAD, TPI-1. Several enzymes or putative loci, viz., ADK, FRK, AMP-1, and TPI-2, were not scored because of faint or inconsistent staining. Phosphoglucomutase, PGM-2, was absent or did not stain in all populations of *Bealia* and was not included in the analysis. All plants examined possessed enzyme bands of identical mobility for GPT-2 whereas GPT-1 and PGI-1 were monomorphic for different alleles in *B. mexicana, M. argentea,* and *M. lucida* and were not included in the genetic analysis except when generating the Wagner tree. Only segregating loci were used to determine the genetic variation in populations, taxa, and F-statistics (Tables 3, 4). The following non-segregating loci that were fixed for a pair of different alleles were removed from the analysis: *B. mexicana* (AAT-2, MDH-1, MDH-2, MDH-3, PGD-1), *M. argentea* (AMP, MDH-1, MDH-2, PGD-1), and *M. lucida* (AAT-2, MDH-1, MDH-2, PGD-1, PGI-2).

Intraspecific allele frequencies at 17 variable loci are given in Table 2. Population allele frequencies, fixation indices per polymorphic locus, and interpopulational genetic identity values can be obtained from PMP upon request. Observed alleles per polymorphic locus per taxon ranged from two in AAT-3, ACO-1, ACO-2, and GDH to five in MDH-2. The greatest number of alleles per locus observed in any population was four (*M. lucida 8029* for MDH-2). Seven, five, and two unique alleles were detected in *B. mexicana, M. argentea,* and *M. lucida,* respectively (Table 2). Three of these unique alleles were present in all individuals surveyed of *B. mexicana* (AMP-2c, MDH-1b, and PGI-a) and one unique allele was present in all individuals of *M. lucida* (PGD-2a).

The mean number of alleles per locus (A) within populations ranged from 1.1 to 1.8 and the mean proportion of polymorphic loci (P) within populations ranged from 0.14 to 0.60 (Table 3). The mean heterozygosity direct count estimate (H) within populations ranged from 0.143 to 0.297, indicating a moderately high level of heterozygosity at most polymorphic loci and in most populations. The mean fixation index (F) within populations or inbreeding coefficient was 0.073 and −0.010 in two different populations of *M. argentea* indicating no significant deviation from Hardy-Weinberg expectations. All other populations ranged from −0.186 to −1.000, suggesting a high excess of heterozygotes relative to Hardy-Weinberg expectations.

Partitioning of genetic diversity within *B. mexicana, M. argentea,* and *M. lucida* was determined using F-statistics where the fixation index within populations (F_{IS}) ranged from −0.079 to −0.867 (Table 4). The amount of genetic diversity among populations within each species (F_{ST}) ranged from 0.142 to 0.192. In *M. argentea* the genetic diversity was partitioned slightly higher among populations (F_{ST} = 0.158) versus within (F_{IS} = −0.079). In contrast, in *B. mexicana* and *M. lucida,* the primary component of F_{IT} was F_{IS} (−0.540 and −0.867, respectively) with the F_{ST} values being very small (0.192 and 0.142). This indicates greater heterogeneity within populations of *B. mexicana* and *M. lucida* than among them. The overall fixation index (F_{IT}) ranges from −0.079, i.e., approaching Hardy-Weinberg equilibrium, to −0.602, indicating a large excess of heterozygotes relative to Hardy-Weinberg expectations.

Genetic identities among populations of each species demonstrate a high level of similarity, ranging from 0.95 to 0.98 whereas identities between species are 0.57 between *B. mexicana* and *M. lucida,* 0.59 between *M. argentea* and *M. lucida,* and 0.83 between *B. mexicana* and *M. argentea* (Table 5).

A Wagner tree (Fig. 1) summarizes the interpopulational relationship based on gentic distance values. Three species belonging to the genus *Chaboissaea* (*C. decumbens, C. ligulata,* and *C. subbiflora*)

Table 2. Intraspecific allele frequency data for 17 polymorphic loci among *Bealia mexicana*, *Muhlenbergia argentea*, and *M. lucida*.

Locus	Allele	*B. mexicana*	*M. argentea*	*M. lucida*
AAT-1	a	0.000	0.013	0.000
	b	1.000	0.948	0.000
	c	0.000	0.039	1.000
AAT-2	a	0.475	0.012	0.000
	b	0.490	0.000	0.500
	c	0.035	0.988	0.500
AAT-3	a	1.000	0.936	1.000
	b	0.000	0.064	0.000
ACO-1	a	0.900	1.000	0.112
	b	0.100	0.000	0.888
ACO-2	a	0.725	0.585	1.000
	b	0.275	0.415	0.000
AMP-2	a	0.420	0.500	0.214
	b	0.035	0.000	0.000
	c	0.545	0.000	0.000
	d	0.000	0.500	0.786
GDH	a	1.000	0.469	0.003
	b	0.000	0.531	0.997
IDH-1	a	1.000	0.906	0.000
	b	0.000	0.094	0.914
	c	0.000	0.000	0.086
MDH-1	a	0.000	0.500	0.500
	b	0.500	0.000	0.000
	c	0.500	0.500	0.500
MDH-2	a	0.060	0.168	0.000
	b	0.440	0.332	0.000
	c	0.000	0.332	0.500
	d	0.500	0.000	0.448
	e	0.000	0.168	0.052
MDH-3	a	0.000	0.006	0.004
	b	0.500	0.367	0.537
	c	0.500	0.627	0.459
PGD-1	a	0.495	0.500	0.500
	b	0.500	0.500	0.500
	c	0.005	0.000	0.000
PGD-2	a	0.000	0.000	1.000
	b	0.975	0.967	0.000
	c	0.025	0.033	0.000
PGI-2	a	0.510	0.000	0.000
	b	0.490	0.777	0.448
	c	0.000	0.153	0.494
	d	0.000	0.070	0.058
PGM-1	a	0.295	0.000	0.503
	b	0.495	0.506	0.497
	c	0.210	0.449	0.000
	d	0.000	0.045	0.000

TABLE 2.   CONTINUED

Locus	Allele	B. mexicana	M. argentea	M. lucida
SAD	a	0.000	0.147	0.000
	b	0.765	0.853	1.000
	c	0.235	0.000	0.000
TPI-1	a	0.010	0.000	1.000
	b	0.960	1.000	0.000
	c	0.030	0.000	0.000

were designated as outgroups based on their morphological simi-
larity to the study species and similar base chromosome number
($x=8$) with *B. mexicana*. All populations of each respective species
form a clade; populations of *M. argentea* and *B. mexicana* showed
the least genetic distance between species (Fig. 1).

DISCUSSION

Populations of *B. mexicana, M. argentea,* and *M. lucida* possess
moderately high levels of genetic variation comparable to that found
in outcrossing and mixed mating plant species (Hamrick et al. 1979).
This is reflected in the mean heterozygosity levels per species of 19

TABLE 3.   GENETIC VARIATION IN POPULATIONS AND TAXA OF *BEALIA MEXICANA,
MUHLENBERGIA ARGENTEA,* AND *M. LUCIDA*: SAMPLE SIZE (n); MEAN NUMBER OF ALLELES
PER LOCUS (A); MEAN PROPORTION OF POLYMORPHIC LOCI (P); 95% CRITERION, MEAN
HETEROZYGOSITY (H), DIRECT COUNT ESTIMATE; AND MEAN FIXATION INDEX (F).

Taxon & coll. no.	n	A	P	H	F
Within populations					
B. mexicana 7946	25	1.6	0.43	0.294	−0.408
B. mexicana 7981	25	1.5	0.43	0.297	−0.474
B. mexicana 8090	25	1.6	0.50	0.234	−0.189
B. mexicana 8264	25	1.3	0.29	0.206	−0.686
M. argentea 8044	25	1.8	0.60	0.205	−0.010
M. argentea 8066	27	1.7	0.60	0.185	−0.142
M. argentea 8248	26	1.5	0.40	0.172	0.073
M. lucida 7973	26	1.1	0.14	0.143	−1.000
M. lucida 7978	26	1.1	0.14	0.143	−1.000
M. lucida 8029	25	1.3	0.29	0.191	−0.520
M. lucida 8039	26	1.4	0.36	0.277	−0.736
M. lucida 8083	26	1.2	0.21	0.157	−0.702
M. lucida 8202	24	1.2	0.21	0.164	−0.652
M. lucida 8249	25	1.3	0.29	0.286	−1.000
Within taxa					
B. mexicana		1.5	0.41	0.26	−0.49
M. argentea		1.7	0.53	0.19	−0.03
M. lucida		1.2	0.24	0.19	−0.80

TABLE 4. SUMMARY OF F-STATISTICS AND UNIQUE ALLELES (PARENTHESIS INDICATES PRESENCE IN ALL INDIVIDUALS) WITHIN POPULATIONS OF *BEALIA MEXICANA*, *MUHLENBERGIA ARGENTEA*, AND *M. LUCIDA*.

Taxon	F_{IS}	F_{IT}	F_{ST}	Unique alleles
B. mexicana	−0.540	−0.244	0.192	7 (3)
M. argentea	−0.079	0.091	0.158	4
M. lucida	−0.867	−0.602	0.142	2 (1)

to 26% and the predominantly negative mean fixation indices per species (0.073 to −1.000) indicating a heterozygote excess (Table 3). Although all three species are limited to a particular edaphic habitat, *M. argentea* which is known only from two localities and has the most restricted range, exhibits the lowest mean fixation index of −0.03, showing no deviation from Hardy-Weinberg expectations. Likewise, the more widespread perennial, *M. lucida* exhibits the highest excess of heterozygotes (F = −0.80) relative to Hardy-Weinberg expectations. The somewhat restricted annual, *B. mexicana*, is intermediate with a mean fixation index of −0.49 but higher direct count, mean heterzygosity (H = 26%). These results do not lend support to the theoretical prediction that species with limited ranges will exhibit lower levels of genetic polymorphisms (Drury 1974; Hamrick et al. 1979; Karron 1987; Karron et al. 1988), although these values could be attributable to the decreasing number of population samples in each respective species. Even though these three species are currently known from very few populations, their genetic diversity is unusually high, and again this could be attributable to the paucity of sampling. However, a similar situation was also found in the highly restricted *Helianthus praecox* Engelm. & Gray ssp. *hirtus* Heiser where the genetic diversity at isozyme loci was similar to the widespread *H. praecox* ssp. *runyonii* Heiser (Rieseberg and Doyle 1989).

Bealia mexicana and *M. lucida* show little genetic differentiation among populations (F_{ST}) but exhibit high values of variability within

TABLE 5. MEAN GENETIC IDENTITY VALUES (NEI 1972) AND RANGES FOR PAIRWISE COMPARISONS OF POPULATIONS OF *BEALIA MEXICANA*, *MUHLENBERGIA ARGENTEA*, AND *M. LUCIDA*.

Taxa	*B. mexicana*	*M. argentea*	*M. lucida*
B. mexicana	0.96 (0.95–0.99)	0.83 (0.79–0.86)	0.57 (0.52–0.66)
M. argentea		0.95 (0.94–0.96)	0.59 (0.52–0.68)
M. lucida			0.98 (0.96–1.00)
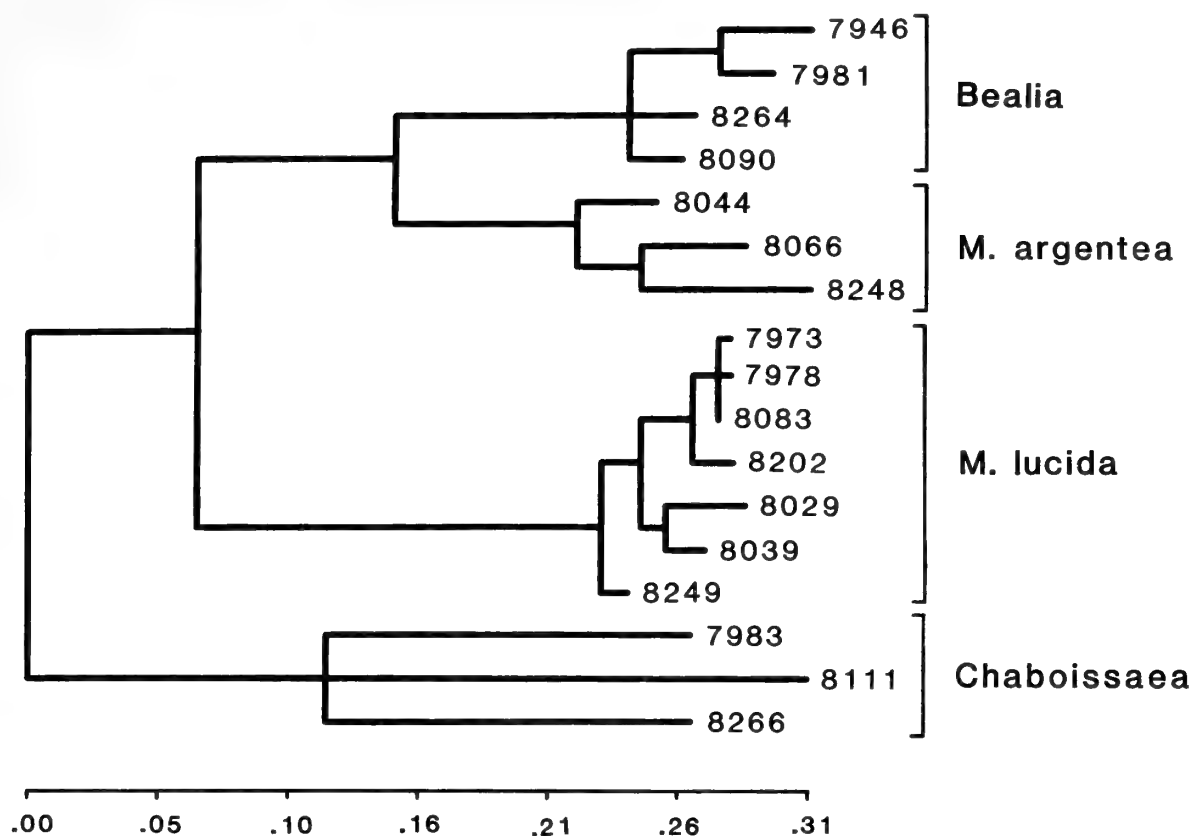
Fig. 1. Wagner tree showing the genetic distance among *Bealia mexicana, Muhlenbergia argentea,* and *M. lucida. Chaboissaea decumbens, C. ligulata,* and *C. subbiflora* were designated as outgroups. Correlation coefficient = 0.99; length = 1.5; numbers refer to population collections given in Table 1; scale indicates distance from root.

populations (Table 4). Again, the highest levels of genetic heterogeneity reside within populations of the more widespread *M. lucida* (F_{IS} = −0.867), followed by the somewhat restricted *B. mexicana* (F_{IS} = −0.540). Although many species of *Muhlenbergia* and other eragrostoid species are often weedy, these two species occupy very restricted habitats that are relatively undisturbed by man. The genetic diversity of *B. mexicana* and *M. lucida* seems to support Loveless and Hamrick's (1984) hypothesis that stable, long-lived population structure of a non-weedy plant species reduces differentiation among populations and increases variability within populations.

In contrast to the uniform levels of electrophoretic variation observed within populations of *B. mexicana* and *M. lucida,* the distribution of genetic variation within *M. argentea* differs markedly. A major portion of the genetic variation in *M. argentea* resides among populations rather than within. This could be a consequence of a small sample size, genetic drift, and/or founder effects (Loveless and Hamrick 1984).

The interspecific mean genetic identity values (Table 5) within each of the three species is similar to values reported among populations (I = 0.95) of other plant species and the mean identities among the three taxa are more similar to genetic identities reported

for congeneric plant populations (I = 0.67) (Gottlieb 1981; Crawford 1983). The results indicate that for genes coding for soluble enzymes, *M. lucida* is genetically distinct from *B. mexicana* (I = 0.57) and *M. argentea* (I = 0.59). By possessing a deeply bilobed lemma with rounded to obtuse lobes *B. mexicana* and *M. argentea* appear morphologically most similar and indeed their pairwise mean identity value is the highest among the three species at 0.83. Although the base chromosome number of *B. mexicana* and *M. argentea* is not concordant, their high genetic similarity indicates a close relationship. These data suggest that *M. argentea* should be placed in *Bealia* or that the recent reinstatement of *Bealia* is unwarranted. Results from a cpDNA restriction site survey among the Eragrostideae genera of the New World indicates that *Bealia* is more closely aligned with *Blepharoneuron* by sharing three parallel site losses than with *Muhlenbergia* (Duvall et al. in review). More data from a thorough sampling within *Muhlenbergia,* specifically from cpDNA restriction site analysis, will perhaps shed some light on this question (Peterson unpublished data).

The Wagner tree (Fig. 1) allows the interpretation of interpopulational relationships and aligns all populations within a species in a separate clade. Due to the very infrequent occurrence of natural populations of these three species, population samples were not always widely spaced geographically. Sympatric populations of *B. mexicana* (*7946, 7981*) and *M. lucida* (*7973, 7978*) occurred within 3.2 km of each other and indeed, within each species pair, show the least genetic distance from one another. However, two populations of *M. argentea* (*8044, 8066*), separated by only 2.3 km, are genetically distant. The other population of *M. argentea* (*8248*) is more than 115 km distant but is genetically more similar with *8066*.

In summary, *B. mexicana* and *M. lucida* have high levels of within population genetic variation often associated with highly outcrossing plants and *M. argentea* has slightly higher genetic variation among populations. Even though *M. argentea* and *B. mexicana* are species with very restricted ranges and different life forms, the genetic diversity of their soluble enzymes is high. At present the only threat to the survival of *B. mexicana* and *M. argentea* is loss of habitat due to human interference. Since two populations of *B. mexicana* and all three known populations of *M. argentea* occur in National Parks, their continued survival at this time is not in jeopardy. Populations of *Bealia mexicana* and *M. argentea* show a higher level of allozymic similarity than either do with *M. lucida.* Other studies have indicated that *Muhlenbergia* is morphologically very diverse and is perhaps polyphyletic (Correll and Johnston 1970; Peterson et al. 1989; Peterson and Annable 1990, 1991, 1992). A complete re-evaluation of all the species within *Muhlenbergia* analyzing mor-

phological and cpDNA variation is in progress which will shed further light on the proper alignment of *M. argentea*.

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ATRIPLEX MINUTICARPA (CHENOPODIACEAE), A NEW SPECIES FROM EASTERN UTAH

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Abstract

Atriplex minuticarpa, a new annual species from Eastern Utah is described and illustrated. The new species appears to be restricted to the Tununk-Shale Member of Mancos Shale in Emery, Grand and Wayne Counties of Utah. It is morphologically closest to *A. powellii* but differs in its divaricate-branching habit, densely imbricate, sessile leaves, small fruiting bracts and utricles, and monoecious inflorescenses with staminate and pistillate flowers in mixed glomerules.

This distinctive new annual species of *Atriplex* was discovered by the first author, 3 May 1985, on a south-facing gentle slope at the base of the Tununk Shale Member of Mancos Shale, 6 mi S of Floy Station, T23S R18E S4, 4500 ft elevation, Grand Co., UT. Review of annual *Atriplex* species in several herbaria (ASC, BRY, CAS, COLO, CS, DAV, GH, IDS, MO, MONT, NY, OC, RENO, RM, RSA, TEX, UC, UNM, US, UT, and UTC) showed only two other previous collections of the new species: *J. G. Harris 855,* 4 Jun 1980 (UTC) and *S. L. Welsh 23241,* 3 Nov 1985 (BRY). Both of these collections were labelled *A. powellii.*

Atriplex minuticarpa Stutz & Chu, sp. nov. (Fig. 1).—Type: USA, Utah, Grand Co., 3 mi E of Green River, T21S R17E S19, gentle south-facing slope, Tununk Member of Mancos Shale, 4000 ft (1219 m), 10 Nov 1988, *H. C. Stutz 9547* (holotype, BRY).

Herbae annuae, 10–45 cm altae, caulis erectus, ramosus a basi ad apicem, ramis inferiis late divaricatis ad angulum 50°–90°, ramis superiis ad angulum 20°–45° patentibus. Folia alterna, dense disposita, deltato-ovata usque orbiculari-ovata, imbricata, 5–15 mm longa, 5–15 mm lata, aliquantum succulenta et caesio-virides, apice acuta vel breviter acuminata, basi late cuneata usque leviter cordata, integra, sessilia, utrinque dense furfuracee farinosa, venae inconspicuae. Flores monoecii, staminati et pistillati flores in mixte glo-
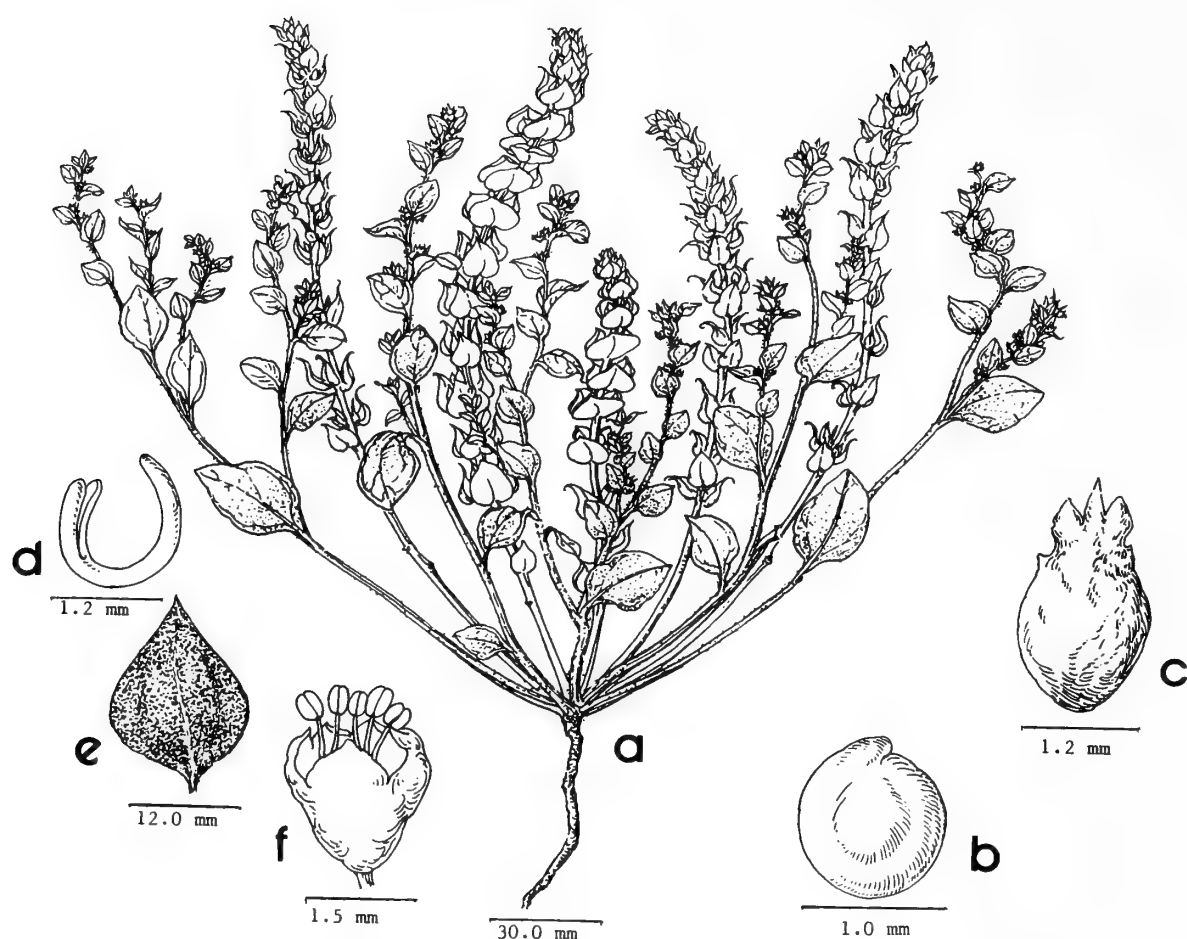
FIG. 1. *Atriplex minuticarpa.* a. Habit. b. Seed. c. Fruiting bract. d. Embryo. e. Leaf. f. Male flower. (Drawings by Xia Quan.)

merulos, axillares. Staminatorum florum perianthia obovata, circa 1.5 mm longa, 5-lobata, segmentis saepe deltatis, membranaceis, stamina 5, antheris circa 0.7 mm longis, plerumque purpurale-rubris, filamentis antheris leviter longioribus. Pistillatorum florum bracteolae connatae fere ad summia, stigmata 2, 1–1.5 mm longa, styli inconspicuo, fructiferi bracteae ovato-oblongae, 1.5–2 mm longa, apeice 3 dentiformibus emergentiis, medianus eo leviter magnior, utrinque plerumque absque appendicibus. Utriculus ovatus usque orbicularis, semen 1–1.2 mm diam., testa membranaceae, flavi-bruneola, radicula supera (Fig. 1).

Annual herbs, 10–45 cm tall. Stems usually erect, ramified from base to top, often purple-reddish; lower branches diverge at wide angles (50°–90°), upper branches diverge at acute angles (20°–45°). Leaves alternate to densely imbricate, deltoid-ovate to orbicular-ovate, 5–15 mm long, 5–15 mm wide, somewhat succulent and blue-greenish, entire, acute to short acuminate at apex, broad-cuneate to slightly cordate at base, sessile, densely scurfy on both surfaces, Kranz-type venation, veins inconspicuous. Flowers monoecious, staminate and pistillate flowers in mixed glomerules in axils of most leaves. Perianth of staminate flowers 5-lobed, segments nearly deltoid, obovate, ca. 1.5 mm long, membranaceous; stamens 5, anthers

ca. 0.7 mm long, usually purple-reddish, filaments slightly longer than anthers. Bracteoles of pistillate flowers fused to near summit; stigmas 2, 1–1.5 mm long; style inconspicuous; fruiting bracts ovate-oblong, 1.5–2 mm long, 1–1.5 mm wide with 3 dentiform emergences at apex, the middle one slightly larger, usually without appendages on surfaces. Utricle ovate to orbicular; seed 1–1.2 mm in diam.; testa membranaceous, yellow-brown; radicle superior. Chromosome number: $2n=18$. Flowering period: May to July.

ADDITIONAL COLLECTIONS: USA, Utah Emery Co.: 11 mi SW of Green River, Hwy I70, mi 149, T21S R14E S35, 5 Jun 1992, *H. C. Stutz 95635* (BRY); ca. 11 mi W of Green River, T22S R14E S22, 4000 ft, 3 Nov 1985, *S. L. Welsh 23242* (BRY); San Rafael Swell, Little Wild Horse Mesa, T26S R10E S19, 4650 ft, 4 Jun 1980, *J. G. Harris 855* (UTC); Green River, southwest edge of town, T21S R16E S17, 15 Sep 1992, *H. C. Stutz 95680* (BRY); 3 mi SW of Green River, occasional patches of 50–100 plants in draws between S facing slopes, T21S R15E S24, 4100 ft, 8 May 1991, *H. C. Stutz 95491* (BRY); 5 mi SW of Green River, T21S R15E S26, 16 May 1991, *H. C. Stutz 95502* (BRY); 10 mi SW of Green River, T22S R15E S17, 9 May 1991, *H. C. Stutz 95492* (BRY); 10 mi W of Green River, Hwy I70, mi 149, T21S R14E S35, 5 Jun 1992, *H. C. Stutz 95635* (BRY); ca. 11 mi W of Green River, T22S R14E S22, 4000 ft, 3 Nov 1985, *S. L. Welsh 23242* (BRY); San Rafael Swell, Little Wild Horse Mesa, T26S R10E S19, 4650 ft, 4 Jun 1980, *J. T17S R13E S24, 21 Jul 1992, *H. C. Stutz and S. C. Sanderson 95657* (BRY); 6 mi SW of Goblin Valley State Park, Little Wild Horse Cnyn., T26S R10E S21, 23 Sep 1992, *H. C. Stutz and S. C. Sanderson 95712* (BRY); ¼ mi N of Muddy Creek on Tununk Shale, T26S R9E S23, 23 Sep 1992, *H. C. Stutz and S. C. Sanderson 95714* (BRY); SE side of Muddy Creek, Tununk Shale, T26S R9E S27, 23 Sep 1992, *H. C. Stutz and S. C. Sanderson 95715* (BRY); Grand Co.: 3 mi E of Green River, T21S R17E S19, 16 May 1989, *H. C. Stutz 95169* (BRY); 4 mi SE of Green River, T21S R17E S30, 3 May 1990, *H. C. Stutz 95485* (BRY); 5 mi SE of Green River, T21S R17E S29, 16 Apr 1992, *H. C. Stutz and M. R. Stutz 95605* (BRY); 7 mi SE of Green River, T21S R17E S33, 5 Sep 1992, *H. C. Stutz 95681* (BRY); 6 mi S of Floy Station, T22S R18E S33, 3 May 1985, *H. C. Stutz 9418* (BRY); 6 mi S of Floy Station, T23S R18E S4, 1 Sep 1988, *H. C. Stutz and G. Chu 94796* (BRY); 6 mi S of Floy Station, T23S R18E S4, 13 Jun 1989, *H. C. Stutz and M. R. Stutz 95195* (BRY); 1 mi N of Moab Airport, Tununk Shale, T23S R19E S11, 14 Jun 1992, *H. C. Stutz 95637* (BRY); 5 mi SE of Thompson, T22S R20E S2, 20 Jul 1992, *H. C. Stutz and S. C. Sanderson 95652* (BRY); Wayne Co.: 20 mi NW of Hanksville, ½ mi S of Wayne–Emery Co. line, T27S R9E S10, 23 Sep 1992, *H. C. Stutz and S. C. Sanderson 95717* (BRY); Neilson Wash, 5 mi SE of Factory Butte,

Fig. 2. Tununk Shale 4 mi E of Green River, Grand Co., UT, the formation on which almost all populations of *Atriplex minuticarpa* have been found. a. Tununk Shale Member of Mancos Shale. b. Ferron Sandstone member of Mancos Shale that caps the Tununk Shale.

T22S R9E S12, 23 Sep 1992, *H. C. Stutz and S. C. Sanderson 95718* (BRY); 2 mi E of Caineville, Hwy 24, Mile 106, T28S R9E S14, 23 Sep 1992, *H. C. Stutz and S. C. Sanderson 95719* (BRY); 6 mi SW of Caineville, Hwy 24, T29S R8E S2, 23 Sep 1992, *H. C. Stutz and S. C. Sanderson 95720* (BRY); 10 mi W of Hanksville, S side of Fremont River, Tununk Shale, T28S R10E S20, 23 Sep 1992, *H. C. Stutz and S. C. Sanderson 95722* (BRY).

DISTRIBUTION AND HABITAT

Atriplex minuticarpa is primarily restricted to the Tununk Member of Mancos Shale in eastern Utah (Fig. 2). It usually grows in small, dense populations, each covering a few hundred square meters, containing 30 to 50 plants per square meter. These small populations are often found contiguous to clay slopes that are devoid of vegetation.

Associated species. Atriplex minuticarpa usually grows as a monoculture but sometimes there are present a few plants of *Atriplex corrugata, A. powellii, Eriogonum inflatum, Euphorbia fendleri, Halogeton glomeratus,* or *Salsola australis.*

Phenology. Flowering and fruiting: Mostly April and May but summer storms often promote prolonged growth and new seedlings that flower as late as mid-August. During June and July most plants on the slopes mature, produce seed, and die while those in draws, where there is more moisture, often remain green and continue to grow for several more weeks.

Atriplex minuticarpa superficially resembles *A. powellii* Wats. and has been previously collected as such. However, *A. minuticarpa* differs from *A. powellii* in habit, leaves, flowers, and fruiting bracts. In contrast to *A. powellii, A. minuticarpa* has a shorter stature (10–20 cm vs. 20–100 cm); its branches are more widely divergent (50°–90° vs. 10°–30°); its leaves are smaller (5–10 mm long, 5–8 mm wide vs. 10–35 × 8–30 mm), usually single-veined instead of prominently 3-veined and they are mostly sessile and densely imbricate instead of petiolate; its fruiting bracts are much smaller (2 mm long × 1 mm wide vs. 3–4 mm long and wide), and are non-appendaged instead of prominently appendaged; and its flowering habit is monoecious, with male and female flowers borne together in axillary glomerules, instead of dioecious.

Plants of *A. minuticarpa* grown in a greenhouse and in a nursery at Brigham Young University, Provo, UT, maintained all of their distinctive characteristics.

BOLANDER'S CLOVER IN THE CENTRAL SIERRA NEVADA: A SENSITIVE SPECIES?

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ABSTRACT

Trifolium bolanderi Gray. (Fabaceae) is endemic to the central Sierra Nevada of California. Commonly called Bolander's clover, it is a federally designated Category 2 taxon for which sufficient data to support a listing as threatened or endangered are lacking. It occurs within a narrow elevational band in mountain meadows of Mariposa, Madera, and Fresno Counties. To learn more about Bolander's clover, its site characteristics, and its restricted distribution we surveyed all known populations. Concurrently, we examined adjacent sites without the species. Sites with Bolander's clover were like those without it in aspect and degree of shade and in soil texture, bulk density, water, and organic matter. Normal hydrologic regimes occurred on 93% of the Bolander's clover sites; and some, still grazed by livestock, had large clover populations. No plant taxa had a positive interspecific association with Bolander's clover. One species, another clover, was negatively associated with it, suggesting intrageneric competition as a controlling influence. Detailed research on nutrient requirements and availability and soil water relationships may point to characteristics restricting Bolander's clover distribution.

Sensitive plant and riparian area management are priority concerns of land managers. Within the state of California, 20% of 187 endangered, threatened, or rare native plants occur in moist or wet habitats (California Department of Fish and Game 1987). Eleven National Forests in California list 44 sensitive plants occurring in federally managed riparian/meadow ecosystems.

All species for which information is needed cannot be studied simultaneously, but knowledge gained by study of selected ones may facilitate research and management of similar species or those occupying similar habitats. This paper reports an initial effort on one species, a clover.

Bolander's clover, *Trifolium bolanderi* Gray. (Fabaceae) (Fig. 1) is endemic to meadows of the central Sierra Nevada in Yosemite National Park and the Sierra National Forest in California. The type location of Bolander's clover is Westfall Meadow in Yosemite, and it occurs within a narrow elevational band (2134 m to 2165 m) in Mariposa, Madera, and Fresno Counties (Jepson 1951). According to park and forest records, there are only 20 meadows with known populations (when this study started). The plant is glabrous, has reflexed flowers with lavender corollas, has decumbent or ascending stems (10- to 23-cm long) that are caespitose on a branched root-

FIG. 1.   *Trifolium bolanderi* Gray. (Bolander's clover).

crown (Jepson 1951, Munz 1970), and reproduces vegetatively as well as by seed.

Bolander's clover is designated by the U.S. Fish and Wildlife Service as a Category 2 taxon for which there is a lack of conclusive data to support a proposed listing as threatened or endangered, and it is categorized by The California Native Plant Society as a "list 4 species" which has limited distribution but low vulnerability (California Department of Fish and Game 1992). It is categorized as a "sensitive" plant species—rare, but found in sufficient numbers and distributed widely enough that, at this time, potential for extinction is low (Sierra National Forest 1991). Both the Sierra National Forest and Yosemite National Park maintain inventories of locations, and inventory data are cataloged by the Natural Diversity Data Base through the Natural Heritage Division of the California Department of Fish and Game.

There are no current plans to list Bolander's clover. Nevertheless, it occurs on grazed forest ranges, and its sensitive categorization may influence land use planning, even though little or no research has been done supporting its status determination, ecology, or response to management.

Given the lack of research, we do not know why Bolander's clover distribution is limited, whether its populations are declining or ex-

panding, and how best to manage land use in areas where it is subject to grazing disturbance.

Bolander's clover was selected for study because of the logistics of reaching meadows with known populations. Also, along with *Trifolium longipes* Nutt. (longstalk clover) and *T. monanthum* Gray. (carpet clover), Bolander's clover was expected to initially increase with overgrazing (Ratliff 1985). Observations related to that study suggested that Bolander's clover prefers wet sites on cool slopes where snow remains until late spring, but those observations also suggested that a shortage of such sites was not a limiting factor.

Logically, study of a species should start with learning about sites where it does and does not occur. Toward that objective and in hopes of identifying factors that limit the distribution of Bolander's clover and justify a sensitive categorization, we surveyed meadow sites with and without that species.

Methods

From late May through August 1990 we surveyed 69 sites in the 20 meadows known to have Bolander's clover and 12 sites with that species in meadows where it had not previously been reported. Adjacent sites in the same meadows but without Bolander's clover were also surveyed. In all, sites in 32 meadows were studied: 10 meadows were protected from livestock grazing in Yosemite National Park, and 22 meadows were subject to grazing on the Sierra National Forest.

Sampling. Meadow hydrology and the influence of grazing largely determine botanical composition, and with aspect, shade, and elevation may serve as key indicators defining ecological sites where Bolander's clover can occur. Aspect, shade, hydrology, and elevation were recorded for sites with Bolander's clover to question the earlier observation that it prefers cool wet sites. Also, the number of Bolander's clover plants was subjectively assessed, and whether the meadow was subject to grazing by livestock was noted. Sites with low shade received sun all day, those with moderate shade received sun from about 9 a.m. to 4 p.m., and those with heavy shade received sun from about 10 a.m. to 2 or 3 p.m. Hydrology evaluations followed the six meadow hydrologic classes of Ratliff (1985). Those classes were: Raised-convex—a site (with an enclosed open water surface) occurring as a mound above the surrounding meadow; hanging—a site that occurs on a slope and is constantly watered by flows from springs and seeps; normal—a site that obtains water from the water table, is recharged by precipitation, and may dry in the surface during summer; lotic—a site that is characterized by moving water and constantly watered by flows from upstream; xeric—a site that occurs on a slope or bench, is seasonally recharged by precipitation

and becomes quite dry during summer; and sunken-concave—a site that is characterized by ponded water and is seasonally recharged by flows from upstream.

At each site containing Bolander's clover, a single 40- × 40-cm quadrat was randomly located on the longest axis and near the site center. The quadrat was placed on the surface and then flipped over left or right depending on a coin toss, and a second paired quadrat was randomly placed left or right of the first on a site without Bolander's clover.

Within each quadrat all rooted species were recorded to determine patterns of interspecific association. At a fixed point on each quadrat frame hits on litter, moss, plants, and bare soil were recorded to learn if major differences occurred in soil surface characteristics between quadrats with and without Bolander's clover.

Soil classification contributes to the definition of an ecological site. Most meadow soils do not have pedogenic horizons, however. Consequently, the 0- to 20-cm depth has been used as a standard for classifying and comparing meadow sites (Ratliff 1985). Near the center of each quadrat, readings of soil temperature were taken at depths of 5 cm and 10 cm. A small-diameter (1.9 cm) core (volume = 48.5 cm^3) was extracted from a depth of 0 cm to 17 cm for determination of soil water and bulk density. The cores were sealed in cans, and wet and oven-dry (105°C for 48 hours) weights were estimated in the laboratory. A large-diameter (5.1 cm) core was collected from the same depth to estimate soil texture and organic matter content. Soil separates were analyzed by the hydrometer method (Bouyoucos 1936). Organic matter content was estimated by weight loss after 6 hours at 600°C.

Statistical analyses. The hypothesis that the numbers of sites with Bolander's clover having different aspects, shade levels, and hydrology were equal was tested by Chi-square with $\alpha = 0.05$. The hypothesis of equal proportions of quadrats with and without Bolander's clover having a particular species or surface characteristic was rejected when the 95% confidence interval for the difference in proportions failed to cover zero (Dixon and Massey 1957). The hypothesis that the difference in a soil property between quadrats with and without Bolander's clover was zero was tested by paired t-test with $\alpha = 0.05$.

RESULTS

Site characteristics. We found the species in meadows from 2073 m to 2226 m elevation.

The 81 sites with Bolander's clover did not occur in equal numbers on all aspects ($\chi^2 = 26.4$, with 4 df). The majority of sites occurred on flat (33%) and south (31%) aspects. Occurrence on north-facing

aspects was 23%, and east and west aspects together comprised about 13% of the sites.

Degree of shading during the day was statistically unrelated to the number of Bolander's clover sites ($\chi^2 = 4.1$, with 2 df). Nevertheless, 42% were in low shade, 35% were in moderate shade, and 23% were in heavy shade.

Bolander's clover appears to favor sites of the "normal" meadow hydrologic class (Ratliff 1985). Ninety-three percent of the sites with Bolander's clover—far more than expected by chance ($\chi^2 = 171.9$ with 3 df)—occurred under that hydrologic regime. Hanging (3%), lotic (3%), and xeric (1%) sites comprised the remainder.

Plant numbers were estimated to vary from less than a hundred to several hundred thousand. Nearly half of the sites were characterized by populations numbering in the 1000's.

Associated species. Positive association between species may exist when they are favored by similar abiotic and/or biotic factors of the habitat but their resource requirements are not competing. Among 43 species reported, none occurred on a higher proportion of quadrats with Bolander's clover than without it than was expected by chance. Negative association may exist when species are found in the same quadrat less often than expected. Only one species, longstalk clover, occurred on a significantly greater proportion (40% vs. 20%) of quadrats without Bolander's clover than on quadrats with it (Table 1). These results suggest that Bolander's clover is not associated with a particular species or group of species, apart from other meadow species. While Bolander's and longstalk clovers may occur in the same quadrat, their indicated association was negative.

No major differences were found in surface characteristics between quadrats with and without Bolander's clover. The proportion of quadrat pairs with hits on the same surface characteristic (70.8%) was greater than expected by chance. Average percentages of surface characteristics over all quadrats were: litter, 10.4%; moss, 12.5%; plants, 62.5%; and bare soil, 14.6%.

Soil properties. The soil properties examined did not differ significantly between quadrats with and without Bolander's clover (Table 2). Soil textures were sandy loams—the average for meadow soils over a large part of the Sierra Nevada (Ratliff 1985). Organic matter content was also about average for the depth range sampled.

DISCUSSION AND CONCLUSIONS

The suggestion that Bolander's clover prefers wet sites on cool slopes (hanging hydrology) with long-lasting snow cover was not substantiated by the known population. Rather, Bolander's clover occurred with 4 hydrologic classes, primarily, the normal class.

TABLE 1. OCCURRENCE OF 15 SPECIES OR GROUPS IN QUADRATS WITH AND WITHOUT BOLANDER'S CLOVER IN THE CENTRAL SIERRA NEVADA. Number of quadrat pairs = 81, and quadrat size = 40 cm × 40 cm. * Significantly different (P = 0.95) from quadrats with Bolander's clover.

| | Number of quadrats | |
Species	With	Without
Carex nebraskensis Dewey.	27	30
C. species L.	29	30
Eleocharis pauciflora (Lightf.) Link.	11	16
Grass species	5	10
Hypericum anagalloides Cham. & Schlecht.	19	17
Ivesia unguiculata Gray.	10	8
Juncus oxymeris Engelm.	13	15
Mimulus primuloides Benth.	42	44
Muhlenbergia filiformis (Thurb.) Rydb.	7	6
Perideridia bolanderi (Gray.) Nels. & Macbr.	8	5
Phalacroseris bolanderi Gray.	11	15
Polygonum bistortoides Pursh.	17	22
Trifolium longipes Nutt.	16	32*
Trifolium monanthum Gray.	5	9
Viola macloskeyi Lloyd.	16	20

Bolander's clover occurs in meadows grazed by livestock for over 100 years and in meadows ungrazed for at least that long. A tendency toward a more decumbent growth habit was observed and the smallest populations (less than 100 plants) occurred on grazed sites. Nevertheless, where grazing use appeared to be moderate, the populations were healthy, and sites with the largest populations (10,000 plants or more) all occurred on grazed meadows. As a management option, therefore, total protection from livestock grazing does not appear necessary. A study of morphological and physiological re-

TABLE 2. SOIL PROPERTIES OF QUADRATS WITH AND WITHOUT BOLANDER'S CLOVER IN THE CENTRAL SIERRA NEVADA. Number of quadrat pairs = 81, and quadrat size = 40 cm × 40 cm. * 95% confidence interval of the difference by paired t-test.

| | Quadrats | | |
Property	With	Without	Difference*
Texture	Sandy loam	Sandy loam	
Sand (%)	61.7	62.8	−1.11 ± 1.90
Silt (%)	31.3	30.5	0.82 ± 1.67
Clay (%)	7.0	6.7	0.30 ± 1.04
Temperature (°C)			
5-cm depth	15.2	15.1	0.11 ± 0.30
10-cm depth	14.6	14.4	0.17 ± 0.23
Water (%)	69.6	72.2	−2.57 ± 7.65
Organic matter (%)	15.3	16.1	−0.85 ± 1.81
Bulk density (g/cm³)	0.89	0.88	0.01 ± 0.05

sponses to defoliation will be needed in order to evaluate hypothetical responses to frequency and season of livestock grazing.

This study failed to reveal biological reasons for the limited distribution of Bolander's clover. It was not associated with any one species or species group which might tie it to a specific association. The indicated negative association of Bolander's clover and longstalk clover may result from the two species occupying similar ecological niches.

Bolander's clover occurred under varied environmental situations, even near the type location in Yosemite National Park, and meadow sites with it did not appear to possess unique characteristics. Their soils and other abiotic factors were representative of many meadow sites in the central Sierra Nevada; elevation remains the only identified unique parameter. We thus hypothesize that Bolander's clover has a high ecological amplitude with regard to environmental variables.

Differences between sites with and without Bolander's clover may be quite subtle, however, and thereby have escaped detection. A more detailed analysis of plant community structure and hydrologic regimes and analysis of nutrient requirements and availability and soil pH, therefore, may reveal why Bolander's clover has restricted distribution.

We found 37.5% of the 32 meadows known to contain populations of Bolander's clover, during this study. Given our present state of knowledge, the meadows themselves are likely more sensitive than Bolander's clover. Constancy of hydrology is a key determinant of plant species in meadows (Allen-Diaz 1991; Hormay 1943). Therefore, we suggest that maintaining the ecological integrity of the meadows through appropriate management will maintain viable populations of Bolander's clover. Managers should strive to keep the sod intact and, thereby, prevent accelerated erosion and preserve meadow hydrologic regimes.

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ANNOUNCEMENT

SOUTHWEST BOTANICAL SYSTEMATICS SYMPOSIUM

The Ninth Annual Southwestern Botanical Systematics Symposium will be held May 28–29. This year's topic is "Plant Reproductive Biology." Invited speakers include William L. Crepet, Cornell University; W. Scott Armbruster, University of Alaska; John F. Addicott, University of Alberta; Elizabeth M. Lord, University of California, Riverside; Allison Snow, Ohio State University, C. Thomas Philbrick, Rancho Santa Ana Botanic Garden. The evening address will be given by Robert Ornduff, University of California, Berkeley.

The cost to attend is $50.00 per participant ($45.00 per student). This includes the Friday evening social, continental breakfast, boxed lunch, and banquet dinner on Saturday. To register, send your name, address, and telephone or Fax number, with a check for the proper amount payable to Rancho Santa Ana Botanical Garden. Mail these to the following address: RSABG, Systematics Symposium, 1500 North College Avenue, Claremont, California 91711. There will be no refunds after May 14, 1993. For more information, please call (909) 625-8767, ext. 251. Be sure to register early as space is limited.

NOTES

FERNS OF LAVA BEDS NATIONAL MONUMENT, SISKIYOU COUNTY, CALIFORNIA.—Alan R. Smith, University Herbarium, University of California, Berkeley, CA 94720, C. Don MacNeill and Christopher Richard, Oakland Museum, Oakland, CA 94607.

As part of an inventory being conducted by Janet Sowers and the Cave Research Foundation of the lave-tube caves of Lava Beds National Monument, eastern Siskiyou County, California, we visited the monument in June 1992 in order to collect and identify the pteridophytes occurring there. The northeasternmost extreme of the monument, including Fern Cave (the only cave mentioned in this report that is not in Siskiyou Co.; see below), extends about 1.5 km into northwestern Modoc County. Because the vegetation in this semi-desert region is Sagebrush Scrub and the soil extremely porous, ferns are able to grow only at the entrances to and bottoms of caves, which are really portions of partially or completely collapsed to nearly intact lava tubes. Sufficient light enters through openings in some of the tubes to allow ferns and non-vascular plants, but no seed plants, to flourish. Temperatures in some of the deeper and more enclosed caves are a relatively constant 50–60°F, and sufficient moisture enters through the openings or percolates through the rock to enable normally forest-dwelling species such as *Polystichum* and *Dryopteris* to attain full size and fertility.

The deepest cave known to contain ferns (Fossil Cave) requires a 50-foot rappel through the narrow opening to reach the bottom, while one of the other more spectacular caves (Fern Cave, ca. 150 m east of the Siskiyou Co. line in Modoc Co.) is now gated and locked at the top to prevent vandalism of the ferns and despoliation of a Modoc sacred site. Permission and assistance from officials of the monument are required to gain entry to both of these caves, but many other caves are open to the public. We gratefully acknowledge the help of monument staff, Gary Hathaway, Chief of Interpretation, and Pat Toops, Chief of Resources Management, in exploring and collecting at these sites.

Applegate (American Midland Naturalist 19:334–368, 1938) previously reported the presence of *Pentagramma triangularis* (Kaulf.) Yatskievych et al. (as *Gymnogramma triangularis*) and *Cystopteris fragilis* (L.) Bernh. at entrances to a few caves, and Erhard (Plant communities and habitat type in the Lava Beds National Monument, California, M.S. thesis, Oregon State University, 1979) further noted *Woodsia scopulina* D. Eaton and *Polystichum munitum* (Kaulf.) C. Presl at the entrances to and within the caves.

As a result of our survey, we report here five additional ferns for the monument, two of them disjunct by a least 200 km from the nearest known populations of the same species. Three of the five represent redeterminations of material already present in the Lava Beds herbarium, while the other two represent new discoveries during our visit. Vouchers of all newly collected specimens have been deposited in the herbaria of the University of California, Berkeley (UC), the Oakland Museum (OAKL), and Lava Beds National Monument (LABE, unofficial abbreviation). Applegate and Erhard specimens are in LABE. Smith collections were made 4–6 June 1992.

Adiantum capillus-veneris L.—A single sterile plant was found growing on the walls of Fossil Cave, about 15 feet above the floor of the cave (*Smith 2543*). It is the first collection from the monument. The locality is about 240 km north of the nearest known populations in Butte Co. (*Austin s.n.,* UC, as cited by Howell and Long, The Four Seasons 3:1–18, 1970; also *Ahart 4236,* UC). The species has not been found in Oregon or Washington, but is recorded from the vicinity of Fairmont Hot Springs in British Columbia, Canada.

Cheilanthes gracillima D. Eaton—A single clump was found growing in crevices of a cliff at the entrance to Blue Grotto, Cave Loop road, ca. 1500 m (*Smith 2538*). This is the first collection from the monument. The nearest site known to us for the species is near Medicine Lake (*Whitney 3484*, UC), about 20 km to the south. In adjacent Modoc Co., it has been found in the Big Valley Mts., about 50 km to the south-southeast (*Bartholomew 6343*, CAS).

Cystopteris fragilis (L.) Bernh.—This is the most common fern at the entrances to caves, and, when in a dried or partly dried condition, it can be easily confused with *Woodsia oregana*. It is also the commonest fern throughout northeastern California. We collected it at Garden Bridges Cave (*Smith 2536*; also *Applegate 10254*), Fool Catcher Cave (*Smith 2543*) and saw it at several other sites; it is also known from Post Office Cave (*Erhard s.n.*), Valentine Cave (*Applegate 10244*), and between Three Sisters and Indian Well (*Applegate 10324*).

Dryopteris arguta (Kaulf.) Maxon—This has been collected once, at the entrance to Jack William Cave (21 July 1940, *collector unknown, s.n.*, LABE), a cave which monument officials are unable to relocate on maps. Nearest known localities are in Humboldt Co., more than 200 km distant (five collections in UC).

Dryopteris expansa (C. Presl) Fraser-Jenkins & Jermy—Hundreds of plants of this species cover the floor of Fern Cave (*Erhard s.n.*; *Smith 2533, 2534*), with the largest plants being nearly five feet tall and fully fertile. The largest plants are about three meters directly below the opening, which is a hole about two meters in diameter. Plants become gradually smaller toward the fringes of the population and are mere sporelings a few cm tall at the periphery, where light is very reduced. The same species was also found in relative abundance in Fossil Cave (*Smith 2540, 2541*), about 14 m below the opening at the top of the cave. This is the first report for the monument and a range extension from the nearest known localities in coastal Humboldt and Del Norte counties of about 200 km.

Pentagramma triangularis (Kaulf.) Yatskievych, Windham & Wollenweber subsp. *triangularis*—This grows at the entrance to Fool Catcher Cave (*Smith 2545*), Fern Cave (*Erhard s.n., Applegate 10245*), and Valentine Cave (*Applegate 10245*). Nearest known localities are in Shasta Co. just north of Redding (*Rose s.n.*, JEPS) and western Siskiyou Co. along the Scott River (*Parker 532*, UC), both over 100 km distant.

Polystichum munitum (Kaulf.) C. Presl—This is the most abundant fern in Fossil Cave, reaching 1.5 m tall and fully fertile (*Smith 2542*). We also found it in Chest Cave (*Smith 2539*), and there is an historical record from Fern Cave (1978, *Erhard s.n.*), although it does not grow there now. The nearest known site we have seen is in western Siskiyou Co., NE of Seiad Low Gap, *Palmer 982* (UC), ca. 120 km to the west.

Woodsia oregana D. Eaton—This species was found at the entrances to many of the larger caves, e.g., Garden Bridges Cave (*Smith 2537*), mostly in partially dried-up condition. Herbarium records exist from Fern Cave (*Applegate 10246*, previously determined as *Cystopteris fragilis*), but we did not find it there. The nearest sites known to us are from Burney Falls, Shasta Co., ca. 75 km to the south (*Baker & Nutting s.n.*, UC), and from near Parker Creek, Modoc Co., ca. 100 km east (e.g., *Howell 11974*, CAS).

Woodsia scopulina D. Eaton—More than a hundred plants were found growing in full to partial sun on the side of Kirk White Cave, 1350 m (*Smith 2535*; *Erhard s.n.*); the species is also known from Lava Cliffs (*Applegate 10265*, previously determined as *Cystopteris fragilis*) and has been collected on the sides of Mt. Shasta, *Cooke 30292* (UC), ca. 60 km southwest. Jepson (Manual of the flowering plants of California, 1923) recorded this species from Modoc lava beds, but we have not found the source of this record in JEPS, UC, or CAS.

Most of the fern species occurring in Lava Beds National Monument appear to be somewhat disjunct from the nearest known populations of the same species. Only three (*Cystopteris, Cheilanthes,* and *Woodsia scopulina*) of the nine species of ferns known from Lava Beds have been collected from the slopes of Mt. Shasta, about 60

km distant (Cooke, American Fern Journal 29:105–111, 1939; American Midland Naturalist 23:497–572, 1940), and only three (*Cystopteris, Cheilanthes,* and *Woodsia oregana*) are known with certainty from Modoc Co. from sites other than Fern Cave in the monument (Bruce Bartholomew in litt.). Whether these Lave Beds disjuncts are a reflection of the unusual habitats provided by the lava caves or the paucity of collections in areas of northeastern California is not known at this time, but they do emphasize the need for further collecting in this part of the state, particularly in habitats that remain relatively moist or cool throughout the summer.

We thank Bruce Bartholomew for helpful comments on this paper.

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REDISCOVERY AND NOTES ON THE STATUS AND IDENTIFICATION OF *CASTILLEJA NERVATA* (SCROPHULARIACEAE) IN THE UNITED STATES.—Mark Egger, 9521 49th Avenue NE, Seattle, WA 98115.

The status of the taxon, *Castilleja cruenta* Standl. (=*C. nervata* Eastw.), has been a matter of some discussion among resource managers and botanists in the Southwest for a number of years. Originally collected on 2 September 1907 by J. W. Blumer [*2133* (NY! *ex* NMC)] on a "rocky spur north of Wilgus Ranch", growing on "rhyolite" at an altitude of "6,000 ft.", the species was described by Standley in 1909 (Muhlenbergia 5:82). Although Standley noted that the "Wilgus Ranch" was in the Chiricahua Mountains in Cochise Co., AZ, very little was known about either the species or its type locality until recently. Standley cited only the single Blumer collection, which has remained the sole definitive collection from Arizona. Kearney and Peebles (Arizona Flora, 2nd ed.:789, 1960) cited a specimen "supposed to have been collected between Fort Huachuca and the San Pedro River (*Mearns 1539*)" that they say "may belong here". This specimen, the location of which appears to be unknown, remains unverified. W. T. Johnson (Desert Plants 8(4):147–191, 1988) cited a specimen (*11242*) he collected on Webb Peak in the Pinaleño Mountains, but this specimen and several other recent collections originally identified as *C. cruenta* have since been annotated as either *C. austromontana* Standl. & Blumer, *C. lanata* A. Gray, or *C. tenuiflora* Benth. [S. Rutman, U.S. Fish & Wildlife Service (USFWS), personal communication].

The type specimen of *C. cruenta* was annotated as *C. nervata* by N. H. Holmgren (NY!) on 20 April 1983, and *C. cruenta* was formally reduced to synonymy under *C. nervata* by Nesom (Phytologia 72:231–252, 1992). *Castilleja nervata* is a Madrean species not previously thought to occur north of Mexico. Nesom (op. cit.) also referred to *C. nervata* two specimens collected by C. G. Pringle [*8174* (NY), *8175* (NY)] on 25 July 1884 in the Santa Rita Mountains, Santa Cruz Co., AZ, noting that they "are atypical in their shallowly toothed floral bracts but otherwise so similar to *C. nervata* that they must be referred to it". The population(s) from which Pringle collected his plants has yet to be relocated. As Nesom (op. cit.) noted, plants from trans-Pecos Texas identified as either *C. nervata* or *C. latebracteata* Pennell are properly placed in *C. rigida* Eastw., a related but clearly distinct species which also ranges southward into Mexico.

The USFWS lists *C. cruenta* as a Catagory 3A species, a taxon "for which the Service has persuasive evidence of extinction" (55 *Federal Register* 6184), though USFWS personnel informally recognize its synonymy with *C. nervata* (S. Rutman personal communication).

On 22 July 1992, J. Scott of Tucson, AZ, passed on to the USFWS crucial information she obtained from J. Williams of Portal, AZ as to the location of the "Wilgus Ranch", near the type locality of *C. cruenta.* On 20 August 1992, I visited this area,

which is in the vicinity of Turkey Creek in the western foothills of the Chiricahua Mountains. I identified what I believe to be the "rocky spur" referred to by Blumer, whereon I located a single population of *C. nervata,* at an elevation of "6,000 ft.", just as described by Blumer. While I was not able to census the area thoroughly, I observed only 7 plants in one small population occupying no more than 100 sq. m within a much larger area of closely similar habitat.

I collected single stems from several multi-stemmed individuals to serve as vouchers: *Castilleja nervata* Eastw. (Scrophulariaceae). — Cochise Co., AZ, on a rocky, south-facing, grassy slope in pale yellowish rhyolitic soil with scattered *Quercus grisea* and *Bouvardia glaberrima,* just below the SW end of a small ridge system immediately N of Turkey Creek, ca. 1830 m, 20 August 1992, *M. Egger 529* (WTU, ARIZ). More precise locational information is on file with the USFWS office in Phoenix, AZ.

Identification. Upon close examination, this species is easily distinguished from any other *Castilleja* species found in Arizona. The plants are single to few-stemmed (up to four stems on two of the plants I observed), and the stems are unbranched. The abundant villous-hirsute pubescence of the slightly zigzagging stem is distinctive. While Standley (op. cit.) mentioned only crimson for bract coloration, in the field the upper ½–⅔ of the bracts may be pale vermillion, red or crimson. The calyx of this species is unusual. It is entirely green, grading from pale green at the base to deep green in the upper few mm, with very short or non-existent secondary lobes. Standley and the key in Kearney and Peebles (op. cit., p. 787) referred to the primary calyx lobes as "slightly cleft behind, deeply cleft in front (for 7 or 8 mm or twice as deeply as behind)". However, in the plants I observed the primary calyx lobes were subequal, with the abaxial cleft no more than 1–2 mm greater than that of the adaxial side. Moreover, both Eastwood (Proceedings of the American Academy 44:574, 1909) and Nesom (op. cit.) described *C. nervata* as having primary calyx lobes nearly equal in length. The corolla of *C. nervata* is almost completely included at full anthesis, with only the stigma or, rarely, the very tip of the corolla beak extending above the calyx lobes.

Phenology. Most of the plants I observed were in full flower on 20 August, while one or two of the solitary-stemmed plants were just beginning to flower. Flowering in this species in Arizona likely begins in early to mid August, depending on the rains, and continues through most if not all of September. The type collection of *C. cruenta* shows plants in full flower on 2 September.

Status and conservation. This collection is significant as the only verified modern population of *C. nervata* north of Mexico. It is very likely that *C. nervata* occurs elsewhere in Cochise Co. and possibly other counties in SE Arizona and SW New Mexico, but its habitat probably is not visited much by botanists with a sufficient knowledge of the genus to recognize its distinctness.

According to Nesom (op. cit.), *C. nervata* is fairly widespread in the western cordilleras of Mexico. However, until such time as additional populations can be located north of Mexico, *C. nervata* should be considered as an extremely rare species in Arizona and in the United States. The conservation of this species in the United States is also a matter of concern, because the only known population is located on private property. The local plant association in which I observed *C. nervata* seemed to be healthy and not degraded by grazing. However, the site would be easily accessible to domestic animals, and heavy grazing should be regarded as a potentially serious threat, if the land use practices of the present or future owners should change. As with many *Castilleja* species, the stems of *C. nervata* are very brittle and vulnerable to trampling by livestock.

NOTEWORTHY COLLECTIONS

ARIZONA

MIRABILIS TENUILOBA S. Watson (NYCTAGINACEAE).—Yuma Co., Borrego Canyon, vicinity of Borrego Tank, SE side of Tinajas Altas Mountains, locally common in canyon bottom, especially just above the tank, perennials, the leaves succulent and yellowish green, ca. 2 km SSE of Tinajas Altas, vicinity 32°17'30"N, 114°03'W, elev. ca. 460 m, 16 June 1992, *Felger and Broyles 92-613* (ARIZ, ASU, MO, RSA, TEX, UC). Sympatric with *Mirabilis bigelovii* var. *bigelovii*; other associated perennials are *Acacia greggii, Agave deserti* ssp. *simplex, Ambrosia ilicifolia, A. dumosa, Asclepias albicans, Bebbia juncea* var. *aspera, Brickellia atractyloides, Bursera microphylla, Cheilanthes parryi, Crossosoma bigelovii, Ditaxis lanceolata, Echinocereus engelmannii* var. *acicularis, Encelia farinosa, Ephedra aspera, Eriogonum wrightii* var. *pringlei, Fagonia laevis, Ferocactus cylindraceus, Galium stellatum* var. *eremicum, Hibiscus denudatus, Horsfordia newberryi, Hyptis emoryi, Jatropha cuneata, Justicia californica, Larrea divaricata, Lotus rigidus, Machaeranthera pinnatifida* ssp. *gooddingii, Mammillaria grahamii, Nolina bigelovii, Opuntia basilaris, O. acanthocarpa, O. bigelovii, Peucephyllum schottii, Physalis crassifolia, Pleuraphis rigida, Pleurocoronis pluriseta, Prosopis glandulosa* var. *torreyana, Salazaria mexicana, Stipa speciosa, Tridens muticus,* and *Viguiera parishii.*

Previous knowledge. Known from Western Colorado Desert in California (Munz, A flora of Southern California, 1974), the eastern desert slopes of Baja California (Shreve and Wiggins, Vegetation and flora of the Sonoran Desert, 1964) and two adjacent islands (Moran, in Case and Cody, Island biogeography in the Sea of Cortéz, 1983), and as a disjunct population in the Sierra del Rosario in northwestern Sonora (Felger, Desert Plants 2(2):87–114, 1980).

Significance. First collection from Arizona. This population and the one in the Sierra del Rosario, 28 km to the SW, are the only records for this species east of the Colorado River; both are on steep granitic slopes. The species diversity is considerably greater at the Arizona locality and many of the associated plants, including *Mirabilis bigelovii,* are not present in the Sierra del Rosario.

—RICHARD FELGER, Drylands Institute, 2509 North Campbell Ave. #176, Tucson, AZ 85719.

TEUCRIUM GLANDULOSUM Kellogg (LAMIACEAE).—Pinal Co., Picacho Mts., ca. 13 km E of Eloy, T8S, R9E, sect. 15 NE¼, in the drainage of a steep, rocky (granite) canyon, with *Acacia greggii, Hyptis emoryi, Keckiella antirrhinoides,* and *Stachys coccinea,* 880 m, 23 Mar 1992, *J. F. Wiens 92-174 and G. Joseph* (ARIZ, ASU), determined by P. D. Jenkins; T8S, R9E, sect. 19 S½, in a steep, rocky (granite) canyon, with *Cercidium microphyllum, Ephedra nevadensis, Herissantia crispa,* and *Janusia gracilis,* 700 m, 21 Apr 1992, *J. F. Wiens 92-356* (ARIZ, ASU, ASDM); T8S R9E, sect. 27 NW¼, on an exposed granite peak, with *Bouteloua curtipendula, Ericameria laricifolia,* and *Eriogonum wrightii,* 1263 m, 21 Apr 1992, *J. F. Wiens 92-369* (ARIZ, ASU).

Previous knowledge. Previously known from southern California, Baja California, and western Arizona in Mohave Co. (Kearney and Peebles, Arizona flora, 1960) and

in Yuma Co. (Horse Tanks, Castle Dome Mts., 1937 *A. A. Nichols* ARIZ; Cabeza Prieta Tanks, Cabeza Prieta Mts., 1962 *N. M. Simmons* ARIZ).

Significance. A range extension of 235 km ENE of the Cabeza Prieta Mts., and 260 km E of the Castle Dome Mts., into the northeastern Sonoran Desert. First record for this species in Pinal Co.

—JOHN F. WIENS, 16920 W. Placita Manana, Marana, AZ 85653.

CALIFORNIA

SCIRPUS HETEROCHAETUS Chase (CYPERACEAE).—Tehama Co., Wilson Lake near NW shore, S side of Wilson Lake Rd ca. 4 km E of California Highway 36/89, T29N, R5E sect. 28, ca. 1608 m; extensive stand emergent in shallow water near the shore and extending somewhat into the lake, partly associated with *Nuphar polysepalum* Engelm.; 5 Aug 1978, *Rubtzoff 9246* (CAS).

Previous knowledge. Widespread but local in temperate North America where known mainly in the East. West of the Continental Divide it is known only from one collection from western Montana, several from northern Idaho, and one or two from southern Oregon. The supposed occurrence in Washington (Hitchcock et al., Vascular plants of the Pacific Northwest 1:377, 1969) is apparently based on two incorrectly identified specimens (WTU!). The previously published occurrence nearest to California is in southern Oregon: "Swan Lake, Klamath County" (Abrams, L., Illustrated flora of the Pacific States 1:274, 1923); "Swamps, Klamath Co." (Peck, M. E., A manual of the higher plants of Oregon, 2nd ed., 1961, p. 148). The Oregon reports apparently are based on the collection(s): Klamath Co., "Swan Lake Valley, 14 July 1895" (US!), and/or "Chinax Camp, Swan Lake, 14 July 1896" (CAS!, WILLU!), *Elmer Applegate 759.*

Significance. This first California record extends the known range ca. 220 km southward from Swan Lake in Oregon. Swan Lake with the adjacent Swan Lake Valley is located ca. 35 km north of the California border. This rare tule, with spikelets separate, floral scales smooth, stigmas 3, achenes strongly trigonous and prominently beaked, and perianth bristles 4(5) and unequal, is often mistaken for the common *S. acutus* Muhl. ex Bigelow or *S. validus* Vahl (*S. tabernaemontani* Gmelin s. lat.).

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IDAHO, MONTANA AND WASHINGTON

GALIUM PEDEMONTANUM (Bellardi) All. (RUBIACEAE).—IDAHO, Clearwater Co. near Orofino, pasture, T36N R2E SW¼, sect. 27, *L. Puchalski 7-90* (IDW*); Idaho Co. Nez Perce Indian Reservation, 2 km S of Stites along Highway 14, 15 Jun 1988, *R. Old s.n.* (IDW); Nez Perce National Forest, 15 km SE of Lowell along Selway River, June 1987, *R. Old s.n.* (IDW); Lewis Co. S slope Lawyer Canyon, T33N, R2E, sec. 12, common in plots of crupina herbicide trial, 29 May 1991, *L. Lass s.n.* (IDW, WS). MONTANA, Missoula Co., Ninemile Valley 5.5 mi NE of Alberton, 10 May 1974, *V. H. Vincent 127* (ID). [* IDW = Plant Materials Collection, Department of Plant, Soil, and Entomological Sciences, University of Idaho.]

Previous knowledge. Native to southern and central Europe from Portugal to the Ukraine (Tutin et al., Flora Europaea, Vol. 4: Plantaginaceae to Compositae [and Rubiaceae], 1976). It is naturalized in WV, KY, and TN (Fernald, Gray's manual of botany, 8th ed., 1970) and has recently been introduced into the Northwest. The species has become a weed in parts of western MT and northern ID.

Significance. Not included in the Flora of the Pacific Northwest (Hitchcock and Cronquist, Flora of the Pacific Northwest, 1973) due to its recent introduction. A description is given below to aid in identification.

Galium pedemontanum (Bellardi) All., Auct. Fl. Pedem. 2, 1789.
Valantia pedemontana Bellardi, Oss. Bot. 61, 1788.
Cruciata pedemontana (Bellardi) Ehrend., Notes Roy. Bot. Gard. Edinb. 33:396, 1958.

Annual. Stems 1–7 dm tall, erect or ascending, slender, subterete with 4 prominent angles or quadrangular, simple or somewhat branched from the base, rough and adhesive, with small recurved prickles and numerous patent hairs, sometimes only below the nodes; internodes 2–5 mm long. Leaves in whorls of 4, ovate to elliptical, 1.5–3 times as long as broad, strongly reflexed, obtuse to acute, slightly hairy above, hirsutely ciliate along veins of basal ⅓ of leaf below, 1-veined, 3–11 × 2–4 mm, uniformly light yellowish-green; lateral veins obscure; margins revolute. Inflorescence in whorls of short axillary cymes; cymes ebracteolate, much shorter than the subtending leaves, (1–)2–3-flowered; peduncles and pedicels hirsute, 1.5–2.0 mm long, partly deflexed under the leaves, in fruit reflexed but not coalescing nor encircling the fruit. Flowers perfect, actinomorphic, 0.5–1.0 mm long; calyx absent; corolla yellowish-green, rotate, 4-lobed, ca. 1 mm in diameter; ovary inferior; styles united in lower third; stigma capitate. Fruit dry, reniform, dark brown, glabrous but finely warty, 1.0–1.5 mm long, with 1 or 2 oblong-cylindric mericarps.

Galium pedemontanum may be distinguished from other annual members of the genus as listed in Hitchcock and Cronquist (1973) by its cymose inflorescence and leaves in whorls of 4. *Galium bifolium* S. Wats. has leaves in whorls of 2–4 but has solitary flowers. *Galium parisiense* L., *G. aparine* L. and *G. tricornutum* Dandy all have leaves in whorls of 5–8 (Hitchcock and Cronquist 1973).

—Joseph E. Laferriere, Joy D. Mastrogiuseppe, and Richard R. Old, see below.

Bryonia Alba L. (Cucurbitaceae).—IDAHO, Bingham Co., along Interstate 15 north of exit 108, 24 Aug 1986, *Old s.n.* (ID, WS); Lake Co., 0.8 km north of Utah line on Highway 89, *Old s.n.* 23 Aug 1986 (ID, WS); Franklin Co., 3 mi east of Franklin, 19 Aug 1984, *Johnson and Brunsfeld 2248* (ID); 9 mi east of Preston, 20 Aug 1984, *Johnson and Brunsfeld 2278* (ID); Latah Co., 2 mi southwest of Moscow, 27 Jun 1982, *Pantone s.n.* (ID); 5 mi E of Troy, *Claud Lomax s.n.* 10 Sep 1989 (WS); Moscow, 17 Jul 1989, *D. Pavck and R. Ousterhaut s.n.* (IDW*); Moscow, University of Idaho campus, 7 Jun 1990, *R. Old s.n.* (IDW). Oneida Co., 5 mi east of Malad, 18 Aug 1984, *Johnson and Brunsfeld 2211* (ID). WASHINGTON, Columbia Co, Dayton, in city park, 17 Sep 1978, *Radebaugh 1* (WS); same location, 23 Sep 1978, *Mastrogiuseppe et al. 1556* (WS); near Turner, 24 Jul 1972, *Low s.n.* (WS); Walla Walla Co., Lewis and Clark State Park, 3 Sep 1985, *Gary s.n.* (WS); Whitman Co., Alpowa Creek, 8 Mar 1973, *Lewke s.n.* (WS); Pullman, Maple Street, 2 Sep 1991, *Laferrière 2342* (ARIZ, WS); Pullman, near Airport Road, 11 Sep 1985, *Simmons and O'Connell s.n.* (WS); 1.6 km S of Union Center, 1 Jul 1975, *Old s.n.* (WS); 1.6 km S of Wilbur Gultch Rd on Ewartsville Rd, 23 Jul 1983, *Erteeb 874-F* (WS); along highway between Pullman and Moscow, Jul 1986, *R. Old s.n.* (IDW). [* IDW = Plant Materials Collection, Department of Plant, Soil, and Entomological Sciences, University of Idaho.]

Previous knowledge. Native to southern, central, and eastern Europe (Jeffrey, Kew Bulletin 23:441–461, 1969), has been widely naturalized in the northwestern United States within the last 20 years, and has become a common, conspicuous weed in Idaho, Utah, Montana, and southwestern Washington [Northam et al., New weed species and potential weed problems identified in northern Idaho during 1984. In: L. M. Lish (ed.), Idaho weed control research report, pp. 276–278, 1984]. The species tends to spread rapidly once established since the seeds are disseminated by birds

and probably by water flow (Engle, The spread and effect of the vine *Bryonia alba* in Whitman County, Washington. M.S. thesis, Department of Botany, Washington State University, Pullman, 1988).

Significance. The species is not included in the Flora of the Pacific Northwest (Hitchcock and Cronquist 1973) because of its relatively recent introduction. A description is therefore given below to aid in identification.

Bryonia alba L., Sp. Pl. 1012, 1753.

Herbaceous, monoecious, perennial vine to 7 m, hispid-papillose, climbing by means of unbranched tendrils. Roots tuberous. Leaves 5–15(–20) cm long, usually ovate but occasionally broader, cordate at the base, 5-angled or palmately 5-lobed, (1–)1.5–2 times as long as broad, with multicellular trichomes each with a prominent white multicellular base; leaf lobes ovate or triangular, acute to acuminate, sharply dentate, the central 2–3 times as long as the lateral. Staminate inflorescence racemose; pistillate inflorescence in subumbellose fascicles. Flowers: calyx shortly-campanulate, 5-dentate, the teeth subulate to triangular; corolla yellowish- to greenish-white, almost rotate, deeply 5-lobed, the lobes oblong; stamens 3 in staminate flowers; filaments free; two stamens bithecous, the third monothecous, the loculi linear, flexuous; pistillate flowers with 3–5 often almost obsolete staminodes; ovary with 3 placentas; rudimentary ovary lacking in staminate flowers; style nude at the base or inserted on an annular disk, slender, 3-branched; stigmas 3, glabrous; ovules numerous, horizontal. Fruit a black, juicy berry, 7–10 mm in diameter. Seeds 2–6(–8), lacrymate, slightly flattened, approximately 2 mm thick, 3–4 mm wide × 4–5 mm long.

Bryonia alba may have been introduced into North America through commercial seed trade. It was formerly cultivated as a medicinal plant in Europe (Tutin et al., Flora Europaea, Vol. 2: Rosaceae to Umbelliferae, 1968) and was available in 19th century seed catalogs in the U.S. (Mack, R. N., Economic Botany 45:257–273, 1991). It has been present in the Northwest since at least 1970 and is found generally along water courses, on roadsides, and in towns (Engle 1988). The oldest known record from the United States is a collection from New Jersey in the 1880's (Engle 1988). The seeds are apparently bird-dispersed. The fruits are eaten by robins and pheasants, usually in the spring after the fruits have been frozen, although the fruits and roots contain alkaloids toxic to humans (Engle 1988). The vines climb and cover shrubs and small trees and may cause damage to their supporting plants by shading them (Engle 1988).

Bryonia may be distinguished from other northwestern members of the Cucurbitaceae by the following key, modified after Hitchcock and Cronquist (1973):

a   Fruit 7–8 mm in diameter, spherical, juicy; central lobe of each leaf twice as long as lateral lobes, the blade usually deltate to ovate; stamens free . . . . *Bryonia*
a′ Fruit 3–8 cm long, ovate to elliptic, dry at maturity; central lobe of leaf more or less equal in length to lateral lobes, the blade ovate to orbicular; stamens connate
    b   Plants annual; roots fibrous; seeds rough, flattened; flowers 6-merous . . . .
        . . . . *Echinocystis*
    b′ Plants perennial; root large, woody-tuberous; seeds thick, smooth; flowers 5(–8)-merous . . . . *Marah*

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OREGON

BRIZA MAXIMA L. (POACEAE).—Curry Co., Oak Flat, along Illinois River 3 mi up from Rogue River, T35S R11W S29, open stony soil w/ weedy grasses, ca. 55 m, 14

May 1987, *Dimling 5* (ORE); Rte. 101 near Hunter Creek Rd. and mouth of Hunter Creek, ca. 6 air km S of town of Gold Beach, T37S R15W S12 SE¼, ca. 75 plants, occasional weed in vicinity, grassy roadside near ocean, ca. 40 m, 9 Jun 1991, *Zika and Stansell 11178* (NY, OSC); beach access, Airport Rd., town of Gold Beach, T36S R15W S36, naturalized weed, 20 April 1992, *Moore s.n.* (OSC); Lane Co., City of Florence, E side of rd. at N end of Hwy 101 bridge over Siuslaw R., T18S R12W S34, NE¼, dry grassy fill slope above parking area, ca. 10 m, Sep 1990, *B. Newhouse and R. Brainerd 1* (OSC).

Significance. First records outside of cultivation in Oregon.

CAREX SAXATILIS L. var. *MAJOR* Olney (CYPERACEAE). — Wallowa Co., Eagle Cap Wilderness, Wallowa-Whitman National Forest, Frances Lake, headwater cirque of Lake Cr., Lostine River drainage, Wallowa Mts., ca. 12 air km SW of town of Joseph, T3N R44E S18 SE¼ of SE¼ and S19 NE¼, 10–15 clonal plants, ca. 500 stems, peaty boggy saturated shores and creekmouths, sometimes in shallow water on E, S and SW margins of Frances Lake, at timberline, over a variety of bedrock substrates, including Jurassic/Triassic Martin Bridge formation limestone and Hurwal formation sedimentary rocks, associated with mosses, *Eleocharis pauciflorus* and *Equisetum variegatum,* ca. 2350 m, 31 Jul 1992, *Zika and Alverson 11809* (OSC).

Significance. First record for the species and variety in Oregon. Fills a gap in the stated range between Clallam Co., WA and Elko Co., NV (Hitchcock et al., Vascular plants of the Pacific Northwest, part 1: Vascular cryptogams, gymnosperms, and monocotyledons, 1969). Not reported by Peck (A manual of the higher plants of Oregon, 2nd ed., 1961); absent in Mason (Guide to the plants of the Wallowa Mountains of northeastern Oregon, 2nd ed., 1980).

CENTRANTHUS RUBER (L.) DC. (VALERIANACEAE). — Curry Co., S breakwater, E and W of Rte. 101 bridge, mouth of Rogue River, town of Gold Beach, T36S R14W and T36S R15W, est. 20,000–30,000 plants, abundantly naturalized and flowering on rock fill and grassy disturbed bank of river, also a weed in vacant lots in town, full sun, with *Alnus rubra, Baccharis pilularis, Festuca arundinacea, Lathyrus latifolius, Luzula campestris, Melilotus* sp., *Salix scouleriana,* and many weedy herbaceous species, 10–20 m, 9 Jun 1991, *Zika and Stansell 11180* (NY, ORE, OSC, VT); W of Rte. 101 bridge, mouth of Rogue River, town of Wedderburn, T36S R14W, 1000's of flowering plants, 9 Jun 1991, observed by Zika and Stansell; Lane Co., City of Eugene, near Willamette and 6th St., T17S R3W S30, 100 flowering plants, escaped and becoming weedy in cracks in asphalt parking lot and along edge of building, with *Acer circinatum* and *Rubus laciniatus,* 128 m, 27 Jan 1988, *Zika 10444* (ORE, OSC).

Significance. First records outside of cultivation in Oregon. The population at the mouth of the Rogue River has increased dramatically in the last ten years, according to Veva Stansell.

GEUM URBANUM L. (ROSACEAE). — Benton Co., City of Corvallis, Pioneer Park, T12S R5W S2, N side of the Marys River just E of the Southern Pacific Railroad tracks, in shade of *Acer macrophyllum* at edge of mowed grassy area, ca. 67 m, 5 Jul 1992, *Alverson 1598* (OSC); Multnomah Co., City of Portland, NE slope of Sentinel Hill, below junction of Fairmount Blvd. and Marquam Hill Rd., Portland, T1S R1E S9, along dirt track in disturbed second growth forest of *Pseudotsuga menziesii, Acer macrophyllum,* and *Alnus rubra,* with *Geum macrophyllum,* ca. 240 m, 17 Jul 1990, *Alverson 1563* (OSC); Washington Co., Canyon Crest Dr., ca. 2 km SW of Sylvan, T1S R1W, ca. 75 plants, well established weed in hedgerows and garden edges, with *Carex deweyana, Epilobium watsonii* and *Taraxacum officinale,* ca. 180 m, 27 Jun 1991, *Zika and Christy 11226* (OSC).

Significance. First published records of this European species for Oregon. This is a fairly common and well established weed of disturbed forests in the West Hills district of Portland.

JUNCUS TRIGLUMIS L. var. *ALBESCENS* Lange (JUNCACEAE). — Wallowa Co., Eagle Cap Wilderness, Wallowa-Whitman National Forest, Frances Lake, headwater cirque of Lake Cr., Lostine River drainage, Wallowa Mts., ca. 12 air km SW of town of Joseph, T3N R44E S19 NE¼, ca. 30 plants, peaty boggy saturated shore, SW margin of Frances Lake, near treeline, Jurassic/Triassic Hurwal formation sedimentary rocks, associated with mosses, *Carex aurea, C. capillaris, C. scirpoidea, C. subnigricans, Eleocharis pauciflorus, Equisetum variegatum, Polygonum viviparum,* and *Thalictrum alpinum,* ca. 2350 m, 31 Jul 1992, *Zika and Alverson 11808* (OSC).

Significance. First record for this species and variety in Oregon. A circumboreal rush recorded 250 km to the SE in the Sawtooth Mts. of ID by Hitchcock et al. (op. cit.). Not reported by either Peck (op. cit.) or Mason (op. cit.).

JUNIPERUS VIRGINIANA L. (CUPRESSACEAE). — Lane Co., City of Eugene, Willow Creek Natural Area, S of West 18th 0.3 km W of Bertlesen Dr., T18S R4W S3, scattered plants over at least 50 ha., established weed for more than ten years, wet prairie invaded by *Fraxinus latifolia* and other woody plants, ca. 125 m, 9 Nov 1991, *Zika and Alverson 11440* (OSC).

Significance. This is the first record outside of cultivation in Oregon. Ornamental specimens were introduced in the Willamette Valley prior to the 1950's. Apparently bird dispersed and widely though sparsely distributed in the West Eugene area.

LIMNANTHES ALBA Benth. (LIMNANTHACEAE). — Lane Co., along Meadowview Rd., 3.2 km W of Hwy. 99, T16S R5W S25, damp gravelly roadbanks, S aspect, full sun, with *Sanguisorba minor,* ca. 105 m, 27 Apr 1988, *Zika 10473* (OSC); N end of Greenhill Rd., T16S R4W S20, gravelly roadside, ca. 105 m, 23 April 1992, *Zika 11496* (OSC); E side of Hwy. 99, 2.8 km E of Eugene airport, T17S R4W S5, NE¼, and in a continuous population for the next 6 km N to Junction City, est. 30,000 plants, gravelly roadside, ca. 100 m, 29 Apr 1992, *Zika 11508* (OSC); Linn Co., along the W side of I-5, 0.8 km N of milepost 225, T12S R3W S21, growing on the gravelly road shoulder, ca. 80 m, 9 May 1987, *Alverson 1077* (OSC); N side of Tangent Dr. 100 m E of Seven Mile Lane, 4.8 km E of Tangent, T12S R3W S10, 14 May 1988, *Rasmussen 54* (OSC); Marion Co., along Riches Road across from the Victor Point fire station, 8.0 km S of Silverton, T7S R1W S11, roadside fencerow in open grassland, ca. 190 m, 2 May 1987, *Alverson 1069* (OSC).

Significance. First published records outside of cultivation in Oregon; native to California. This species has been bred as an oil-seed crop, and is cultivated on wet clay soils in the Willamette Valley. Roadside populations may be ruderal colonies dispersed by farm machinery or trucks transporting seeds between fields and storage facilities.

TRIFOLIUM ANGUSTIFOLIUM L. (FABACEAE). — Douglas Co., BLM 15.0 Rd., T24S R4W S15, roadside weed, with *Trifolium variegatum,* 14 Jun 1978, *Crowder 417* (Roseburg BLM herbarium); Powell Point, Umpqua River, 1978, M. Thiele obs.; Powell Point, Umpqua River shore, town of Tyee, T24S R7W S30, ca. 75 m, 15 May 1987, *Hopkins et al. M84* (Douglas County Museum); Myrtle Island RNA, Umpqua River at end of Cougar Cr. Rd., 7.3 km W of Bullock Bridge at State Hwy. 138, *Alnus-Fraxinus/Rubus/Phalaris* community, rare, naturalized, 24 Jun 1988, *Thompson et al. 88-1053* (OSC); Hastings Ave., 0.2 km W of Rte. 99, town of Sutherlin, T25S R5W, hundreds of flowering and fruiting plants, sunny waste ground, vernally damp situations, xeric by mid-summer, roadside and disturbed grassy areas N of road, with *Bromus mollis, Cichorium intybus, Festuca arundinacea, Lotus corniculatus, Parentucellia viscosa, Rumex crispus, Vicia cracca* and other weeds, ca. 155 m, 13 Jun 1991, *Zika and Thiele 11206* (NY, ORE, OSC); Lane Co., upper Spencer Creek drainage N of the Lorane Highway just S of the Eugene city limit, T18S R4W S11, near moist draw in open grassland on S facing slope, ca. 230 m, 12 Jun 1991, *Alverson 1583* (OSC); SE margin of Short Mountain landfill, N of Camas Swale Creek,

T18S R3W S36, wetland edges and along service roads, common, ca. 150 m, 6 Feb 1992, *Zika 11447A* (OSC).

Significance. First records for Oregon.

TRIFOLIUM HIRTUM All. (FABACEAE).—Jackson Co., U.S. Army Corps of Engineers Rogue River Project, Applegate Reservoir, W Shore of reservoir, upper Applegate River drainage, 23 air km SSW of Ruch, T41S R4W S2 SW¼ of NW¼, common weed in open second growth woods of *Pinus ponderosa, Pseudotsuga menziesii, Quercus kelloggii, Quercus chrysolepis,* ca. 615 m, 7 Jun 1991, *Zika 11171* (OSC); S shore of E arm of Applegate reservoir, upper Applegate River drainage, 23 air km SSW of town of Ruch, T41S R4W S1 NE¼ of NW¼, ca. 30 plants, weed in open second growth *Pinus ponderosa* woods along hiking trail, with *Bromus tectorum, Madia* sp., *Pseudotsuga menziesii, Quercus kelloggii, Triteleia hendersonii* and *Vulpia microstachys,* ca. 615 m, 10 Jun 1991, *Zika 11193* (NY, OSC); Rte. 238 roadside, town of Ruch, T38S R3W, 100–200 plants, disturbed sunny ground on bank of mowed ditch, ca. 500 m, 7 Jun 1991, *Zika 11172A* (OSC); Corner of Kirtland Rd. (E end) and Pacific Rd., ca. 1 km S of Rogue River, T36S R2W S13, common weed in grassy areas, with *Bromus tectorum,* ca. 365 m, 7 May 1992, *Zika 11527* (OSC).

Significance. First records outside of cultivation for Oregon. Apparently introduced to stabilize roadbanks around Applegate Reservoir during its construction (1976–1980). Now invading open and partially shaded habitats in the vicinity; potentially a troublesome weed.

Field work supported by a grant from the Native Plant Society of Oregon.

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LEPIDIUM HETEROPHYLLUM Benth. (CRUCIFERAE).—OREGON: Benton Co., Corvallis, O.S.U. campus. 21 May 1927, *Hyslop s.n.* (OSC); same locality, 20 Jun 1932, *H.M. Gilkey s.n.* (OSC); Linn Co., Albany, along Interstate Hwy. 5 by a pond formed by Truax Creek, in gravelly soil with *Poa, Rubus, Bromus, Rumex, Chrysanthemum, Daucus,* T10S R3W sect. 33, 60 m, 23 May 1991, *R. R. Halse 4146* (OSC, MO, NY, US); Marion Co., Salem, along Turner Road by Salem Airport, in gravelly, rocky soil with *Rubus, Holcus, Festuca, Bromus, Daucus, Dactylis,* T8S R3W sect. 1 or 12, 63 m, 16 May 1991, *R. R. Halse 4142* (OSC, CAS, MO, NY). WASHINGTON: Pierce Co., about 7 airline miles SW of Puyallup, near the junction of Canyon Rd. E and 176th St. E, gravelly, rocky soil with *Teesdalia, Plantago, Trifolium, Rubus,* T19N R4E sect. 31, 146 m, 8 May 1991, *R. R. Halse 4132* (OSC, NY, MO, WS, WTU).

Previous knowledge. In North America *Lepidium heterophyllum,* a native of western Europe, has been known only from Vancouver Island, British Columbia, Canada (Scoggan, The Flora of Canada 3:835, 1978).

Significance. First record for the United States and a southward range extension of about 430 km from Vancouver Island, B.C.

—RICHARD R. HALSE, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2910.

OREGON AND WASHINGTON

ABUTILON THEOPHRASTI Medic. (MALVACEAE).—OREGON, Multnomah Co., Linnton, near Portland, 28 Sep 1910, *Suksdorf 1632* (WS). WASHINGTON, Klickitat Co., Bingen, Jul 1885, *Suksdorf 1842* (WS); same locality, 10 Oct 1927, *Suksdorf 12355* (WS); same locality, weed in garden, 6 Jul 1924, *Suksdorf 11750* (WS). Kittitas Co., 9 Oct 1989, *C. McKinney s.n.* (IDW*). Lewis Co., Toledo, 7 Sep 1982, *Lampitt*

s.n. (WS); Centralia, 8 Oct 1976, *Magnuson s.n.* (WS). Skagit Co., Sedro Wooley, 23 Sep 1977, *Morgan s.n.* (WS). Thurston Co., Rochester, 31 Jul 1989, *M. McKay s.n.* (IDW); same locale, 28 Sep 1989, *M. McKay s.n.* (IDW). [* IDW = Plant Materials Collection, Department of Plant, Soil, and Entomological Sciences, University of Idaho.]

Previous knowledge. Native to India, southeastern Europe, and the Mediterranean (Tutin et al., Flora Europaea, Vol. 2: Rosaceae to Umbelliferae, 1968; Kearney, Leaflets of Western Botany 7:241–254, 1955). It was cultivated as an ornamental and as a potential fiber crop in the United States and has escaped to become a weed in parts of Washington and Oregon (Roché, Pacific Northwest Extension Publication PNW368).

Significance. Not included in the Flora of the Pacific Northwest (Hitchcock and Cronquist 1973). A description is given below to aid in identification.

Abutilon theophrasti Medic., Künstl. Geschl. Malv.-Fam. 28, 1787.

Herb annual, erect, 25–240 cm tall, from a taproot. Stems cylindric, simple or sparsely branching above, velvety-tomentose with glandular hairs above, pubescent with simple and stellate hairs below. Leaves simple, alternate, stipulate, cordate-orbicular, acuminate, slightly crenate, long-petiolate, green and covered with stellate hairs above and below, 10–15 cm long, 7–20 cm wide. Inflorescence of small cymes of 1–6 flowers in axils of upper leaves; peduncles shorter than petioles but as long as or longer than the flowers; pedicels jointed above middle. Flowers regular, perfect; epicalyx lacking; sepals 5, united to just below middle, the lobes oblong-oval, mucronate, with midnerve prominent at base, densely stellate, often with glandular hairs; petals 5, obovate, yellow to yellow-orange, slightly notched at apex, 7–13 mm long; stamens numerous, the filaments united into a tube for most of their length, the column conic; ovary superior; stigmas terminal, capitate. Fruit a schizocarp; mericarps 12–15, arranged in a single whorl, exceeding the calyx, black, hirsute, with a slender erect to slightly spreading aristate beak, each with several seeds, blackish with a yellowish waxy coat, usually dehiscent in situ and not separating readily from central axis. Seeds reniform, finely tuberculate, ca. 4 mm across.

Abutilon may be distinguished from other genera of the Malvaceae by its hirsute, several seeded mericarps (Tutin et al. 1968). Several other species are known from other parts of North America, from which *A. theophrasti* may be recognized by the latter's tomentose herbage (Kearney 1955).

—JOSEPH E. LAFERRIERE, JOY D. MASTROGIUSEPPE, and RICHARD R. OLD, see below.

WASHINGTON

ANTHRISCUS SYLVESTRIS (L.) Hoffm. (APIACEAE).—Spokane Co., southwest corner of Newman Lake, abandoned hayfield/pasture area, ponderosa pine/Douglas fir forest, T26N R46E sect. 10, 11 May 1990, *Roché and Nielsen 1472* (WS); Whitman Co., north of Colfax, on south side of Crumbacher Rd., between road and pasture, 14 Jun 1991, *Roché 1488* (WS).

Previous knowledge. Native to Europe, North Africa, and temperate Asia and naturalized from Newfoundland and Quebec to New Jersey (Fernald, Gray's manual of botany, 8th ed., 1970). It has recently become established in eastern Washington and classified as a Class A noxious weed in the state (Roché, PNW Extension Bulletin 367, 1991).

Significance. Hitchcock and Cronquist (Flora of the Pacific Northwest, 1973) mention the plant but do not provide a description. A description is given below to aid in identification.

Anthriscus sylvestris (L.) Hoffm., Gen. Umb. 40, 46. t. 1. f. 19., 1814.
Chaerophyllum sylvestre L., Sp. Pl. 258, 1753.

Erect, hairy biennial or perennial herb forming offsets. Roots fusiform, slightly thickened. Stems erect, hollow, deeply furrowed, pubescent at the nodes below, glabrous and branching above. Leaves triangular, 2–3-pinnately compound, somewhat pubescent beneath, slightly pubescent to glabrous above, up to 30 cm long; sheaths with short spreading hairs along nerves; leaflets ovate, pinnatifid and coarsely serrate, with scabrous margins. Umbels compound, terminal, the earliest often overtopped by lateral branches, 2–6 cm in diam.; peduncles (3–)6–12, glabrous, 1–4 cm long; involucre lacking; bracteoles 4–6, ovate, aristate, ciliate, often pink, spreading or deflexed, 2–5 mm long; pedicels about equalling bracteoles at anthesis but elongating at maturity. Flowers 3–4 mm in diam.; calyx minute or lacking; petals white, notched, with an inflexed point, the peripheral slightly elongated. Fruit oblong-ovoid, smooth, 5–10 mm long, with a short beak; commisures constricted; carpels subterete, tapering into a long beak; ridges confined to the beak; styles slender, spreading.

Anthriscus sylvestris may be distinguished from *A. scandicina* (Weber) Mansfeld by the former's short-beaked, ribless fruit.

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REVIEW

The Natural History of Puget Sound Country. By Arthur R. Kruckeberg. 1991. University of Washington Press, Seattle and London. xxiv + 468 pp. $29.95.

Puget Sound country—as defined by Seattle botanist Arthur Kruckeberg, who has lived in it for over four decades—is the 10,000 square mile drainage basin whose waters run into that "grand inland sea . . . so lavishly endowed by Nature," located in northwestern Washington state and southwestern British Columbia. This region includes some of the most spectacular scenery in the hemisphere—the Cascade and Olympic ranges, large freshwater lakes, a complex geology, and the intricate waterways of the Sound itself.

At the time of the first extensive exploration of the Sound by George Vancouver's expedition in 1792, the "audaciously rich cultures" of coastal Indians in the region lived in a state of "accommodation, not overkill" as a way of life. The forests were vast, the rivers and streams pure, and the seas abounded with a seemingly endless supply of food. Kruckeberg argues, however, that this status of apparent harmony with nature stemmed not from an aboriginal "kindness" to the land, but was a consequence of lack of intent or necessity to overexploit local resources. In contrast, the first Europeans to settle in the region early in the 19th century were there precisely to exploit its natural bounty. According to the author, "Puget Sound country after . . . the 1850s was so cataclysmically altered and with such unanimity of purpose that no single voice of conscience would have effectively stemmed the onslaught of the land."

Kruckeberg's intent in this book is not to chronicle the destruction of the biota and landscape of Puget Sound country. Rather, his aim is to describe the natural

history of the region and the effects of its burgeoning population and, ultimately, to give readers "a measure of understanding about the workings of natural systems in the Puget Sound basin. Central to the matter of choosing alternatives is *understanding;* that is the mission of this book." This understanding and appreciation, the author hopes, can lead to "wise decisions and actions to preserve and protect what is left of the . . . basin's natural beauty and wild, self-sustaining life in variety."

Kruckeberg's sweep of natural history is impressively broad. He describes the landscape of the region and its geological nature and history, climate, the marine environment and its inhabitants, terrestrial habitats and their inhabitants, the importance of water in the region for the quality of life, the aboriginal peoples that once populated the basin, and the European impacts on Puget Sound country. Thus, he ranges through geology, hydrology, oceanography, limnology, fisheries, forestry, anthropology, social and economic history, and other disciplines outside the realm of zoology and botany that conventionally defines natural history.

Since I am a native of the Pacific Northwest, have family ties in Seattle, and lived there for two years as Art Kruckeberg's first graduate student, I cannot claim to be completely objective about the general appeal of this book to audiences beyond the Puget Sound region. That the local audience was receptive is indicated by the fact that the first printing of 10,000 copies—large for a university press book—has nearly sold out; hopefully, this may mean that Kruckeberg's important message has reached the influential audience for whom it is intended.

The book's title reflects the provinciality of its setting, but Kruckeberg's perspectives will interest biologists outside Puget Sound country. It is pioneering in its intent and in the vehicle via which this intent is realized. It provides environmentalists, biologists, and others concerned about the declining quality of life with the kinds of arguments and perspectives that can be almost universally employed, arguments that must be accepted and implemented if human populations can ever achieve a modus vivendi with what remains of their natural environment. Herbert Mason, Kruckeberg's doctoral mentor at Berkeley and in recent years a resident of Puget Sound country, long ago emphasized the role of ecological extremes (rather than modes) in determining distribution patterns of plants. Likewise, Kruckeberg describes the biotic impacts of ephemeral but extreme events such as volcanic eruptions, mud flows, climatic change, wind storms, fires, freezes, floods, and the intentional as well as unintentional introductions of alien species. Even the problematic origin of Mima mounds (so named after their "type locality" in the region) merits 14 pages of interesting discussion and analysis. Here and elsewhere, Kruckeberg emphasizes that features such as topography, substrate chemistry, and other local phenomena have a profound effect on the nature of the local biota in a region with a more or less uniform climate. Kruckeberg's aim is to instill "ecological understanding"; though his examples may be regional, the principles they illustrate and the arguments they provide are universal.

This book is gracefully written and its themes are eloquently argued. It is sumptuously illustrated with over 300 photographs, maps, graphs, diagrams, and line drawings. Although it is a model of books that should exist for every metropolitan region of the continent, few, if any, prospective authors are likely to have the combination of intellect, breadth, and dedication required to produce such a book. In the course of exposition, Kruckeberg offers this thought-provoking quotation from *The Fragmented Forest*: "natural resources are not given to us by our fathers, but are loaned to us by our children." Perhaps when this perspective is widely adopted, we can feel that our planet is in good hands.

—ROBERT ORNDUFF, Department of Integrative Biology, University of California, Berkeley, CA 94720.

ANNOUNCEMENT

Biodiversity and System Function in Mediterranean-type Ecosystems

(Synopsis of Symposium held 7–11 September 1992 at
Cape Town, South Africa)

Changes in the global patterns of land-use and climate are currently occurring at a rapid rate. These are resulting in a precipitous loss of species, and extensive transformations of landscapes. This loss of biodiversity is a potential threat to humans. We have evidence that the loss of individual species can have profound effects on ecosystem processes which are important to the maintenance of habitable human environments, such as the transfer and cycling of water, nutrients and energy. We interpret this as a warning that the loss of biodiversity itself may have impacts on ecosystem functioning. Papers presented, together with discussion of the topics covered at the Cape Town symposium, revealed that there is a total lack of data which directly investigate the effects of biodiversity on ecosystem function. A synthesis of available data does, however, provide examples that could be interpreted as support for the notion that a causal relationship between diversity and function holds.

The symposium and subsequent workshop explored the differences between ecosystem function and ecosystem service. The former is seen as the set of processes which maintain natural systems through the transfer of matter, energy and information, while the latter is relative to human dependence on the ability of ecosystems to provide a biophysical basis for human life. Diversity too was investigated, and scale was considered an important baseline consideration for future research into the topic, with the levels of most immediate importance being those of species and landscape.

A discussion of the "functional group" concept concluded that although species perceived to be within such a group may duplicate ecosystem services with regard to one specific purpose, they are not necessarily equivalent with regard to others. We suggest the term specific ecological equivalence to describe such examples to avoid the negative connotations of redundancy and expendability. The other concept which received attention was that of keystone species. We here define them as "species whose presence or absence controls the presence or absence of other species, and hence the biodiversity of the host system".

The challenge for the future, it was decided, is to determine the relationship between the system properties of biodiversity and ecosystem function by establishing an appropriate and tractable research protocol.

Mediterranean-type ecosystems (MTE's) are highly suitable for addressing the questions considered by the symposium. In addition to supporting a long history of ecological research and international collaboration, they draw together the experience and perspective of researchers from both developed and developing countries, and represent a spectrum of systems ranging from pristine natural environments to highly impacted ones. Successful comparative studies of the past endorse this expectation, such as those involving studies of convergence in veg-

etation, and studies of the dynamics of invasion by exotic organisms. Global management of the set of different systems also necessitates consideration of many different goals, and calls upon a diversity of approaches to the solution of environmental problems. Ecosystems of five Mediterranean-type regions are convergent in many respects, and will serve as valuable sites for research processes at a global scale, via both manipulative and natural experiments. The fact that MTE's occur in both the Northern and Southern hemispheres will also facilitate the investigation of global processes, such as temperature rise.

The biologically interesting components of these systems are linked to species richness at different spatial scales. MTE's represent diverse landscapes with high levels of endemism and many species-rich genera. While it may at this stage be impossible to prove utilitarian value for much of the genetic diversity which resides in the global set of MTE's, these systems also contain centers of dense human populations which threaten the conservation of this diversity. This human pressure may pose a threat to the functioning of many of these systems, not only by the attrition of species, but by the transformation of landscapes. Further clarification of the problem, and the development of a tractable international MTE research program is urgently required. Tasks for further synthesis of existing knowledge, and the development of such a program have been assigned to members of the workshop body.

Summary statement of the workshop proceedings: G. Davis, J. Keeley and B. Lamont on behalf of the workshop and symposium participants.

ANNOUNCEMENT

Fourth Symposium on Resources of the Chihuahuan
Desert Region: United States and Mexico

University of Texas at El Paso, September 30–October 2, 1993

CALL FOR PAPERS

The Fourth Symposium on Resources of the Chihuahuan Desert Region: U.S. and Mexico will be held on the campus of the University of Texas at El Paso on September 30–October 2, 1993. The Symposium is sponsored by the Chihuahuan Desert Research Institute, University of Texas at El Paso, Sul Ross State University, and the Big Bend Natural History Association.

The theme for the Fourth Symposium will be "Conservation and Sustainable Development of Chihuahuan Desert Resources". The objectives are: 1) to promote international cooperation between scientists, institutions, agencies, and organizations; 2) to build on previous data by seeking to determine how resources are being used, managed, threatened, and depleted; 3) to provide new information on sustainable approaches to ecological concerns and the preservation of Chihuahuan resources; 4) to expose participants to the scope of current research activities in the region; and 5) to allow for a clear understanding of future research and management priorities. Each presentation will be 18 minutes in length with two minutes for questions.

Presentations can be made in either English or Spanish. Authors will have the option of submitting their paper for publication in the Symposium Proceedings.

Session topics include:

Vertebrate Zoology
Invertebrate Zoology
Ecology
Wildlife Biology
Botanical Sciences
Aquatic and Riparian Habitats
Geology, Paleontology, and Hydrology
Anthropology, Archeology, and Ethnology

Abstracts: Each abstract must be typed double-spaced on an 8½ × 11 sheet of paper. List the author(s), affiliation(s), and current address(es). Abstracts should be no longer than 200 words. Please submit a diskette with a hard copy if possible. All abstracts must be postmarked no later than 15 June 1993.

Send abstracts to: Chihuahuan Desert Symposium, %CDRI, P.O. Box 1334, Alpine, Texas 79831 or call (915) 837-8370 for additional information.

Proceedings of the Symposium

Interface Between Ecology and Land Development in California

Edited by Jon E. Keeley

An outstanding compilation of timely papers by researchers, conservationists, consultants and policy makers, including:

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Contents

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LOSS OF FITNESS RESULTING FROM POLLINATOR EXCLUSION IN *SILENE SPALDINGII* (CARYOPHYLLACEAE)

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Abstract

The importance of pollinator availability to fitness was investigated for *Silene spaldingii,* an endangered, hermaphroditic perennial plant of grasslands in northwest Montana. Proportion of fruits matured, seeds per fruit, germination, seedling growth and seedling survival, were all significantly lower for plants from which pollinators were excluded. The overall reduction in fitness for bagged plants was greater than 99%. Loss of fitness attributable to inbreeding depression was at least 97%. These results suggest that the presence of pollinators is critical to the persistence of *S. spaldingii* at this site. During 65 hours of observation at peak bloom in two different years, *Bombus nevadensis* was the only visitor observed to enter flowers and carry pollen, suggesting that it is one of, if not the only important pollinator at this site. Management activities that threaten pollinator populations should be avoided in order to protect populations of this endangered plant.

Breeding systems in plants range from asexual reproduction and nearly complete selfing to obligate outcrossing (Richards 1986). Many outcrossing species are capable of some degree of self-fertilization, depending on the strength of self-incompatibility mechanisms (Faegri and van der Pijl 1971; Schemske and Lande 1985). However, selfed progeny often suffer from inbreeding depression. In general, the strength of inbreeding depression is proportional to the rate of outcrossing (Allard 1960; Wright 1977) and may be manifest at many different life history stages (Kalisz 1989; Johnston 1992). The importance of pollinators to plant population viability will depend on the extent to which selfing is possible and the magnitude of inbreeding depression.

Silene spaldingii occurs sporadically in mesic grasslands of eastern Washington, adjacent Oregon and Idaho, and northwest Montana. Most of its habitat has been lost to agriculture and livestock grazing. All but five of 41 known populations consist of fewer than 100 plants, and the majority have fewer than 30 plants (Schassberger 1988; Lorain 1991). Extant populations are threatened by livestock grazing, road construction, herbicide treatment and exotic weed encroachment. *Silene spaldingii* is listed as threatened in every state

in which it occurs (Lesica and Shelly 1991) and is a candidate for listing as a threatened or endangered species (C-2) by the U.S. Fish and Wildlife Service (USDI–FWS 1990). The largest known population of *S. spaldingii* (ca. 10,000 plants) occurs in northwest Montana on The Nature Conservancy's Dancing Prairie Preserve. Management options, such as controlled burning, that could affect both *S. spaldingii* and its pollinators are under consideration at this site.

Loss of pollinators could lower fecundity and increase rates of selfing in *Silene spaldingii* which could, in turn, result in decline or even extirpation of small populations. The purpose of this study was to determine the principle pollinators of *Silene spaldingii* on Dancing Prairie Preserve and the effect of exclusion of pollinators on components of fitness.

Species Description

Silene spaldingii Wats. (Caryophyllaceae) is a partially self-compatible, hermaphroditic, perennial taprooted herb, 20–40 cm tall. Rhizomes or other means of vegetative propagation are lacking (Hitchcock and Maguire 1947; Lesica personal observations); reproduction is apparently by seed only. The perfect flowers are 1–2 cm long with white petals that are mostly concealed by the green calyx. Three to twenty flowers are borne at the top of the stem in a sparingly branched, terminal, cymose inflorescence. Fruits are dehiscent capsules containing up to 150 seeds. Seeds require stratification, so germination occurs mainly in the spring. Rosettes are formed the first year, and flowering may occur during or after the second season. Examination of numerous flowers over the course of many years indicates that *Silene spaldingii* is protandrous. Anthers mature and dehisce pollen first. During this time, the styles are unexpanded, and the unexposed stigmatic surfaces are held well below the level of the anthers. After anthers have shed most of their pollen, they shrivel and fall from the filaments. At this time the three styles expand in length, and the stigmas spread apart and become receptive. Each open flower persists for two to several days, and two or more flowers may be in bloom on the same plant, so geitonogamous pollination is possible. This system promotes outcrossing while allowing the possibility of selfing. Plants in Montana begin flowering in early to mid-July and, depending on the year, continue for 2–3 wks. Most fruits are mature by early to mid-August.

Study Site

Dancing Prairie Preserve is in a narrow glacial valley at 825 m, 6 km north of Eureka in northwest Montana (T37N R27W S26). At Fortine, ca. 27 km south and 75 m higher, mean annual precipitation was 438 mm for 1950–1980. Mean July maximum and Jan-

uary minimum were 27.9° and −11.4°C respectively. The preserve consists of grasslands dominated by bunchgrasses in the genera *Festuca, Agropyron* and *Stipa. Silene spaldingii* occurs in patches separated by ca. 50–100 m, most commonly in shallow swales with deep soil and relatively high canopy cover of grasses.

Methods

I monitored a patch of *Silene spaldingii* for pollinators on 12–14 July 1988 and 9–12 July 1990 from the edge of a patch of *Silene spaldingii* with 25–30 flowering plants in plain view. Different patches were observed in the two years. Observation periods were 1–3 hr long and scattered throughout the days but were concentrated more heavily in the mornings and evenings. Because many insects, particularly moths, are crepuscular, I made daily observations for 1–2 hr before sunrise and after sunset. Total observation time was 30 hr in 1988 and 35 hr in 1990.

In order to determine the importance of pollinators to the fitness of *Silene spaldingii,* I selected 35 close-neighbor pairs of plants and randomly assigned members of each pair to treatment or control groups. The inflorescence of each treatment plant was enclosed in a bag made of 1-mm mesh, white nylon and tied at the bottom around the stem with thread. Flowers inside bagged inflorescences appeared to bloom in a normal manner without evidence that the treatment caused microclimatic changes. The occasional flower that had already begun to open was removed before bagging. I bagged plants on 10 July 1990 and collected the inflorescences on 6 August 1990. During this time, cattle or deer destroyed 13 of the treatment plants, leaving 22 pairs intact.

I classified each flower or fruit in each inflorescence as one of the following: (1) flowers, recognized by unwilted petals, styles and stigmas and lack of fruit development, (2) empty fruits, with swollen ovaries but containing only aborted or unfertilized ovules, and (3) developed fruits, with well-formed or developing ovules. Developed fruits were dissected and the number of fully formed seeds counted in those fruits that were mature. In some fruits developing seeds could not be accurately counted; these were excluded from analysis of seeds/fruit.

Mature seeds from bagged and open-pollinated plants were randomly assigned to each of two cold stratification treatments, 4-wk and 8-wk. Seeds were placed on moist filter paper in petri dishes, 15 seeds per dish with 15 replicates of the bagged and open-pollinated seeds for each stratification treatment. Sealed petri dishes were placed in the dark at 4°C. Filter paper was remoistened every 2 wk. After completion of cold treatments, seeds were treated with 14 hr of light daily at room temperature. After seven days I counted the

number of seeds in which the radicle had emerged from the seed coat to obtain germination rate.

I used germinated seed from the 8-wk stratification to assess the performance of seedlings from the two pollination treatments. All 51 of the germinated seeds from bagged plants and 69 randomly-selected germinated seeds from the open-pollinated plants were planted in untreated soil from a nearby grassland that lacked *S. spaldingii*, one to a 3.5 cm-diameter well in 6-well containers. Five containers were placed in each of four pans (blocks). Each pan contained 12 seedlings from bagged plants and 18 seedlings from open-pollinated plants, except one pan had 15 seedlings from bagged plants. Seedlings were grown at 15°C for 14 hr/d under Agro-lites that produced 200 $\mu Em^{-2} s^{-2}$ photosynthetically active radiation at the soil surface. Every third day pans were irrigated to saturation for 8 hr and then allowed to dry for the remaining 64 hr. These conditions were intended to simulate the stressful low-light, periodically dry conditions present in the seedlings' natural habitat. Blocks and pans were spatially randomized at every watering. After 90 days I counted the number of survivors. Plants that failed to produce any expanded leaves were counted as dead. All remaining plants had at least six expanded leaves and appeared to be established. To obtain a measure of juvenile growth, I carefully removed the survivors, washed all soil from their roots, and weighed them.

A t-test was used to assess the effect of pollination treatment on the number of seeds per fruit. Since bagged and open-pollinated plants did not differ significantly in number of flowers remaining at the time inflorescences were collected (t = 0.244, P > 0.80), I estimated percentage developed fruits as the number of developed fruits divided by the number of empty plus developed fruits. These data could not be normalized, so the non-parametric Mann–Whitney test was employed to assess the effect of pollination treatment. I used contingency-table analysis to assess the independence of pollination treatment and seedling survival. The effect of pollination treatment on germination and juvenile growth (live weight) was assessed by analysis of variance (ANOVA). Relative fecundity and fitness are calculated as the performance of progeny from the bagged plants divided by the performance of progeny from open-pollinations. Cumulative fitnesses were estimated by multiplying together the mean fitnesses from components measured (Stevens and Bougourd 1988).

RESULTS

Pollinators. Weather during the 3-d study period in 1988 was generally cloudy, cool and windy, and I witnessed three visits by potential pollinators. On all three occasions I observed a small work-

TABLE 1. RELATIVE PERFORMANCE OF *SILENE SPALDINGII* PLANTS DENIED ACCESS TO POLLINATORS (BAGGED) COMPARED TO OPEN-POLLINATED PLANTS AT FIVE LIFE STAGES. [a] * P < 0.05, *** P < 0.001.

Fitness component	Bagged $\bar{x} \pm$ SD (n)	Open $\bar{x} \pm$ SD (n)	Test statistic	Relative fitness
Fruits developed (%)	13.5 ± 23.6 (22)	58.2 ± 32.9 (22)	U = 91***[a]	0.232
Seeds/fruit	62.6 ± 9.1 (13)	97.6 ± 10.5 (15)	t = 2.48*	0.641
Germination (%) (4 wk cold)	6.7 ± 1.6 (15)	16.9 ± 1.8 (15)	F = 85.8***	0.396
Germination (%) (8 wk cold)	22.7 ± 2.4 (15)	59.6 ± 3.8 (15)	F = 85.8***	0.381
Seedling survival (%)	7.8 (51)	43.5 (69)	χ^2 = 18.34***	0.180
Juvenile growth (mg)	59.0 ± 14.5 (4)	148.5 ± 68.5 (27)	F = 4.79*	0.397

er bumblebee, *Bombus nevadensis*, sequentially enter into the flowers of at least three *Silene spaldingii* plants. In 1990 the weather was sunny, hot and dry, and I again witnessed only three visitations, again all by *B. nevadensis*. Each year I collected one of the *B. nevadensis* visitors, examined it under a microscope, and found pollen that appeared identical to that taken from herbarium specimens of *S. spaldingii* on their bodies, suggesting that these bees are capable of being effective pollinators.

Effects of pollinator limitation and inbreeding. Deleterious effects of excluding flower visitors on components of fitness were apparent at all five stages in which they were measured (Table 1). Some of these effects were probably due to reduced pollination, while others are attributable to inbreeding depression.

Plants denied access to pollinators matured only 28% as many fruits as open-pollinated plants (Table 1). Reduction in developed fruits was likely due to lack of access to pollinators. Protandry makes selfing difficult (Faegri and van der Pijl 1971) but not impossible, and *Silene spaldingii* did set some fruit in the absence of pollinators. Nonetheless, reduced fruit set made a large contribution to loss of fitness of bagged plants.

Fruits from bagged plants contained 64% as many fully-formed seeds as fruits from open-pollinated plants (Table 1). Reduction in the number of matured seeds per fruit could be due to pollen limitation; however, in predominantly outcrossing species, a portion of ovule abortion is often attributable to genetic load (Wiens et al. 1987; Charlesworth 1989; Manasse and Pinney 1991). These two

possible causes cannot be distinguished based on the data collected. Reduction in fitness due to this component was the smallest of those measured.

Germination was greatly enhanced by longer cold stratification (Table 1; ANOVA: F = 133.0, P < 0.001). Germination of seeds from bagged plants was 38–40% of that from open-pollinated plants under both 4-wk and 8-wk cold stratification treatments (Table 1).

Survival of transplanted seedlings from seed of bagged plants was 18% of the survival of progeny from open-pollination (Table 1). Reduction in fitness due to seedling death was greater than for any other measured component. Only four plants from the selfed treatment survived to the end of the study; thus, the confidence interval for growth difference between treatments was large. Since all selfed progeny in one pan died, that block was eliminated from the ANOVA. In spite of the small sample size, the effect of pollination treatment on plant survival was significant (P < 0.05). Furthermore, juvenile plants from selfed seed were 40% as large as those from open-pollinated seed (Table 1). Block and treatment × block interactions were not significant (P > 0.44).

Discussion

Lowered fecundity, inbreeding depression and life history. Poor germination and seedling survival by progeny from bagged plants may have resulted from differences in seed size caused by lower pollen loads or other effects associated with the treatment but unrelated to selfing. However, I did not observe any consistent differences in seed size between the treatments. Furthermore, seed weight is relatively constant in many species regardless of environment (Fenner 1985, p. 21). Although lowered fecundity of bagged plants may have been caused by inadequate pollination, post-zygotic incompatibility or inbreeding depression, decreases in germination, seedling survival and juvenile growth of progeny from bagged plants were most likely due to inbreeding depression.

Some of the seed from open-pollinated flowers may have arisen by selfing. Furthermore, geitonogamy may also contribute to the proportion of selfed progeny from the open-pollinated plants. As a result, some of the progeny of open-pollinated plants were probably the result of selfing; consequently estimates of inbreeding depression may be too low. Results of my experiments suggest that *Silene spaldingii* carries a large load of deleterious recessive genes.

Reductions in fecundity as well as lowered germination, survival and growth all contributed significantly to loss of fitness in *Silene spaldingii* plants denied access to pollinators. The combined effect of pollinator exclusion on fruit and seed production was an 85% reduction in fecundity. Cumulative reduction of fitness in progeny

of bagged plants from germination through the juvenile stage is estimated to be 97%. Assuming these latter effects result from inbreeding depression, this is one of the highest cumulative rates of inbreeding depression reported for flowering plants in spite of my failure to measure reproductive components of fitness in the progeny (Charlesworth and Charlesworth 1987; Sakai et al. 1989). Heterozygous advantage is often more pronounced in stressful conditions (Lesica and Allendorf 1992; Parsons 1971), and those provided in my experiments may have been more severe than under some field conditions but were thought to be more realistic than typical benign greenhouse treatments. The presence of such a large genetic load suggests that *S. spaldingii* is predominantly outcrossed under natural conditions.

Implications for conservation of Silene spaldingii. The process of extinction is often an interaction between demographic and genetic processes (Gilpin and Soulé 1986; Lande 1988). Moderate losses of progeny due to inbreeding depression will usually not affect population viability if fecundity is ample (Shields 1982). Furthermore, the effects of inbreeding depression may even slow the loss of genetic variation in small populations (Lesica and Allendorf 1992). However, reduced fecundity combined with inbreeding depression may lower recruitment to the point where population size declines. As population size declines, extinction from random demographic events or environmental catastrophes becomes more likely (Gilpin and Soulé 1986).

In *Silene spaldingii* the absence of open pollination resulted in lowered fecundity and loss of fitness due to inbreeding depression. Total reduction in fitness is estimated to be greater than 99%. This suggests that the *Silene spaldingii* population could suffer a significant reduction in recruitment if pollinators were severely limited. During 65 hr of observation at peak bloom over two years, *Bombus nevadensis* was the only visitor observed to enter flowers and carry pollen. Thus, it appears that *B. nevadensis* is one, or perhaps the only, significant pollinator of *S. spaldingii* at Dancing Prairie. Periodic burning, herbicide spraying and grazing by livestock or ungulates are common management activities in maintaining grassland reserves. *Bombus nevadensis* nests at or just beneath the surface of the ground (Hobbs 1965) and could be sensitive to these management practices (Sugden 1985; Panzer 1988). Thus, in order to protect the population of *S. spaldingii* at Dancing Prairie, consideration must be given to the survival of this pollinator in any management actions.

In experiments reported here, *Silene spaldingii* showed a large reduction in fitness due to pollinator exclusion and inbreeding depression (Table 1). Many of the remaining populations of *S. spal-*

dingii are small and may be composed of related individuals. In addition, many occur in small habitat islands that may not be large enough to support a population of pollinators. In such cases, inbreeding depression from enforced selfing could reduce population growth, resulting in extinction after only a few generations. In light of these considerations, every effort should be made to protect all remaining large populations, especially those occurring in relatively extensive natural areas capable of supporting viable populations of pollinators.

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ANNOUNCEMENT

CHANGES AT JEPS AND UC
UNIVERSITY OF CALIFORNIA, BERKELEY

Dr. Brent Mishler has been appointed Director of the Jepson Herbarium (JEPS) and the University Herbarium (UC) and Associate Professor in the Department of Integrative Biology at the University of California, Berkeley, effective 1 July 1993. A search for a Curator of the Jepson Herbarium has begun. In late 1993 or early 1994, JEPS and UC will return to campus and will be housed on one level in the renovated Valley Life Sciences Building. Questions about status of the collections during the move or about the curatorship should be sent to: Director, Jepson Herbarium, University of California, Berkeley, California 94720.

PUCCINELLIA HOWELLII (POACEAE) IS GENETICALLY DISTINCT

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Abstract

Population Aggregation Analysis of isozyme variation patterns among North American populations of *Puccinellia* (Poaceae), independent of prior notions of species identity, results in the delimitation of several distinct species, each comprising one or more populations. One of the solitary populations resolved as a distinct isozyme species is the Shasta Co., California, population previously recognized as the sole known population of *Puccinellia howellii* J. Davis. Isozyme variation patterns thus provide independent confirming evidence that this species is distinct.

Every valid description of a new plant species includes a diagnosis, i.e., a summary of the characters by which that species can be distinguished from others. Although the practice of species diagnosis predates the acceptance of organic evolution, it is as relevant today as ever. In the analysis of populations and multi-population systems of sexually reproducing organisms, genetically fixed differences—diagnostic character combinations—constitute direct evidence that one such system is evolutionarily independent of another (Eldredge and Cracraft 1980; Nelson and Platnick 1981; Cracraft 1983, 1989; Nixon and Wheeler 1990; Davis and Nixon 1992). These authors have used the term "phylogenetic species" to refer to population systems that are demarcated by fixed differences, and therefore are the least inclusive entities among which there is character evidence for hierarchic (i.e., non-reticulating) descent, and among which phylogenetic analysis is thus appropriate. Phylogenetic species are not discovered through phylogenetic analysis; like the characters in an analysis, phylogenetic species are basic elements of a phylogenetic analysis, and must be delimited by some other procedure prior to the analysis (see below, and see Davis and Nixon 1992). Thus, the venerable concept of species diagnosis is as significant in terms of evolutionary and phylogenetic theory as it is in the traditional practice of taxonomic species delimitation.

Puccinellia Parl. is one of the more controversial genera in the grass family in terms of species delimitation. Floristic treatments often identify complexes of questionably distinct species (e.g., Hughes and Halliday 1980), and different authors often propose quite dissimilar treatments of the species in the same region, even when they recognize similar numbers of species (e.g., Swallen 1944; Sørensen

1968; Welsh 1974). It has been suggested (e.g., Hitchcock 1969; Welsh 1974) that difficulties encountered in delimiting species of *Puccinellia* are attributable to cleistogamy, which, by enhancing inbreeding, leads to genetic differentiation among populations; and to polyploidy, which helps to stabilize distinctive character combinations.

It is one thing, however, to propose which evolutionary factors have promoted a given pattern of populational differentiation, and another to determine whether a particular group of populations should be recognized as constituting one or more than one species. Objective analysis of existing patterns, as evident in different character sets, can reveal degrees of differentiation, and points of congruence (Mickevich 1978). Isozymes represent a large set of relatively independent and objectively scorable characters (Gottlieb 1977). They have often provided evidence of differentiation between morphologically cryptic and near-cryptic populations and population systems, whether or not these groups were regarded as species (e.g., Wolff and Jefferies 1987; Bruederle et al. 1989; Paris et al. 1989; Gottlieb and Edwards 1992). One objective method for delimiting species according to the criteria of the phylogenetic species concept is Population Aggregation Analysis (PAA; Davis and Manos 1991; Davis and Nixon 1992). PAA aggregates populations into diagnosable units (i.e., phylogenetic species) using any sort of character that can be scored as absent, present and fixed, or present and not fixed within each population. The analysis of any particular character set is conducted independently of previously recognized species boundaries, and PAA therefore generates independent assessments of species boundaries, which in turn allows for tests of congruence between different data sets.

I recently described *Puccinellia howellii* J. Davis in these pages (Davis 1990). This species, known from a series of mineral seeps in Shasta County, and first noted as unique by J. T. Howell, was initially diagnosed, like most vascular plant species, in terms of morphological characters. Here I present evidence of congruence between isozyme characters and the morphological characters that originally justified the recognition of *P. howellii*.

MATERIALS AND METHODS

The present study is part of an ongoing analysis of isozyme variation in *Puccinellia* (Davis and Manos 1991; Davis and Goldman 1993). The sole known population of *Puccinellia howellii* was sampled by collection of seed (i.e., caryopses) from different individuals into separate envelopes. Seeds from these envelopes were sown in separate clay pots and later thinned to leave one plant per pot; the 45 individuals surveyed for isozyme variation therefore represent the offspring of 45 different individuals from the collection site. Seed

Table 1. Isozyme Allele Profiles of Four Isozyme Species of *Puccinellia* in California (See Text). Eighty-three alleles are numbered separately within each diploid locus; 0 = absent; 1 = present, fixed; * = present, not fixed. Fixed differences between species are underlined.

	Aat			Adh	Dia	Idh	Mdh	
	1	*2*	*3*	*1*	*1*	*1*	*1*	*2*
	1234	1234	123456	123456	1234	1234	1234	12
P. howellii	0*10	0100	000100	**0100	0110	0100	0101	01
P. lemmonii	0**0	***0	0*****	00***0	****	0010	**0*	**
P. nuttalliana—1	0110	01*0	0*010*	0*0*00	0*10	0100	010*	01
P. nuttalliana—2	0110	*100	010101	*00100	0110	0110	*101	01

germination, enzyme electrophoresis, and staining of 17 diploid loci (i.e., distinct loci in related diploid species) were conducted as described by Davis and Manos (1991).

Population variation is summarized as a profile in which each allele observed in any population of *Puccinellia* is represented for each population as absent, present and fixed, or present and not fixed (Table 1). The profile of the Shasta Co. population has been analyzed in association with those of more than 100 other populations of North American *Puccinellia* in a single Population Aggregation Analysis (Davis and Manos 1991; Davis and Goldman 1993; Davis unpublished data). As noted above, PAA determines the number and membership of distinct species recognizable on the basis of population variation profiles, and thus provides an independent test of congruence with species boundaries that have been recognized on the basis of other attributes (Davis and Manos 1991; Davis and Nixon 1992). In brief, all populations, regardless of presumed identity, were compared with all others. Any two populations that were not distinct in at least one character (i.e., fixation of an allele in one and absence of the allele in the other) were aggregated (i.e., grouped), and a summary profile of the group replaced those of the constituent populations. Cycles of aggregation were continued until all groups and all ungrouped populations were distinct, and these were recognized as putative isozyme species.

Results

Staining with eleven substrate systems led to the resolution of seventeen presumptive loci among the diploid species of *Puccinellia*, each apparently present in multiple copies among the remaining species, most of which are known to be polyploids (Davis and Manos 1991; Davis and Goldman 1993). Members of the latter group,

TABLE 1. CONTINUED.

Mdh	6-Pgd		Pgi	Pgm	Skdh	Sod	Tpi	
3	1	2	2	1	2	1	1	2
1234567	1234	12345	11 12345678901	123456	123456	123	1234	123
0010000	1100	11000	0001010001*	*10*00	**1000	010	0010	010
00*00*0	**00	****0	00**0***0*0	0*0***	000***	0**	00**	***
0**00*0	1100	01*00	**010*00000	010*00	00*1*0	010	0*10	0**
1010000	1100	01000	000*0*00*00	010*00	000110	010	0110	01*

including *P. howellii,* exhibit the characteristic "fixed heterozygosity" pattern typical of polyploid species (Roose and Gottlieb 1976; Gottlieb 1977). Although a chromosome count has not been obtained for *P. howellii,* the sampled population exhibits at least one fixed allele at each diploid locus, two fixed alleles at each of four loci, and three fixed alleles at one locus, *Pgi2* (Table 1).

With more than 100 populations of North American *Puccinellia* now incorporated into the ongoing population aggregation analysis, the solitary population of *P. howellii* continues to be resolved as distinct. Among other species represented in the analysis are *P. lemmonii* (Vasey) Scribner and *P. parishii* A. Hitchc., the only two diploid species in temperate North America (Davis and Goldman 1993); the predominantly inland *P. nuttalliana* (Schultes) A. Hitchc. complex, within which six isozyme species are resolved (Davis and Manos 1991); the predominantly coastal *P. pumila* (Vasey) A. Hitchc. complex (Davis unpublished data), within which five isozyme species are resolved; and *P. distans* (L.) Parl., *P. fasciculata* (Torrey) E. P. Bicknell, and *P. simplex* Scribn. (Davis unpublished data).

For purposes of comparison, the isozyme profile of *P. howellii* is presented with those of three other western North American species with isozyme profiles similar to that of *P. howellii* (Table 1), and likely to be among its closest relatives. Each of these profiles of a related species represents several populations that have become aggregated during the course of the analysis. *Puccinellia howellii* is distinct from *P. lemmonii* and from isozyme species 1 and 2 of *P. nuttalliana* in 3, 3, and 10 fixed differences, respectively. At least three fixed differences also have been identified between *P. howellii* and every other species of *Puccinellia* that has been delimited, including *P. pumila,* which is similar to it in morphology (Davis 1990; Davis and Manos 1991; Davis and Goldman 1993; Davis unpublished data). *Puccinellia lemmonii,* a diploid species, exhibits a great-

er number of alleles than any other species sampled in this study. To the extent that it has been sampled, *P. lemmonii* appears to be fixed for just one allele (*Idh1*, allele 3), which is absent from *P. howellii*; conversely, *P. howellii* is fixed for two alleles that have not been observed in *P. lemmonii* (*Idh1*, allele 2; and *Skdh2*, allele 3), each of which is present in at least one of the isozyme species of *P. nuttalliana* (Table 1). *Puccinellia howellii* also is fixed for two alleles that do not occur in either of the *P. nuttalliana* isozyme species (*6Pgd2*, allele 1; and *Pgi2*, allele 10), and both of these alleles occur in *P. lemmonii*. Although every allele that is fixed in *P. howellii* and absent from one of the other two species in Table 1 is also present in some other species, *P. howellii* also carries two nonfixed alleles (*Pgi2*, allele 11; and *Skdh2*, allele 1) that have not been detected in any other population of *Puccinellia*.

DISCUSSION

There is considerable interest in the reconstruction of descent relationships among species, as there is in the process of speciation. In recent years phylogenetic analysis has developed into a formal, repeatable methodology involving character state definition, parsimony analysis, and related procedures. There has been less progress, however, towards universally accepted procedures for the delimitation of species. It should be obvious, however, that the results of phylogenetic analyses, as well as those of studies of speciation, introgression, and other processes, are influenced by the initial apportionment of individuals and populations among species. In short, species delimitation should be conducted by explicit procedures; the development of Population Aggregation Analysis is an attempt to achieve this objective. As with other analytical procedures employed in systematics, including phylogenetic analysis, the results obtained reflect the organisms and characters that are sampled, and undersampling introduces predictable biases (Davis and Nixon 1992). Thus, all results are provisional, and subject to the collection of additional data.

However many species an investigator chooses to recognize within *Puccinellia*, the observed situation remains that of a polyploid complex with relatively few diploid species, with pronounced genetic structuring evident within many local populations (Davis and Manos 1991; Davis unpublished data), and with some distinct assortments of isozyme alleles occurring repeatedly across several populations, while other combinations occur in one or only a few populations. The latter situation is exemplified by the Shasta Co. population that has been recognized as *P. howellii*. Thus, the available evidence is consistent with the delimitation of this population as a phylogenetic species, *Puccinellia howellii*. It is resolved as a single isozyme species,

distinct from all other populations sampled, precisely in congruence with its previous delimitation on the basis of morphology.

Every allele that appears to be fixed in *Puccinellia howellii* has been observed elsewhere in the genus, but because this species also carries two unique alleles (neither of them fixed), its isozyme profile cannot be assembled by the summing of those of any known combination of other species. *Puccinellia howellii* may have originated by divergence from a single ancestral species (cf. Gottlieb 1973), or via interspecific hybridization, and it is difficult to rule out either possibility. Under either speciation model the two unique alleles in *P. howellii* might have arisen either before or after the origin of this species. All other alleles known to occur in *P. howellii* also have been observed elsewhere in the genus, but not as a group within any single species. If it is assumed that all occurrences of comigrating enzyme electromorphs (i.e., those that migrate identical distances under the electrophoretic conditions employed) do represent identical alleles, and that all cases of shared alleles between species have been discovered, the hypothesis of speciation without hybridization still cannot be dismissed unless it is further assumed that related species have not lost alleles they once shared with *P. howellii*.

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ANNOUNCEMENT

On 3 August 1993, Dr. Alwyn Gentry, a member of the Missouri Botanical Garden research staff for 21 years, was killed in an airplane crash in western Ecuador. He was 48 years old and leaves behind his wife, Rosa, and three children. He has long been recognized for his knowledge and collections of New World Tropical floras.

ATRIPLEX PERSISTENS (CHENOPODIACEAE), A NEW SPECIES FROM CALIFORNIA

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Abstract

Atriplex persistens, a new annual species from California is described and illustrated. The new species appears to be restricted to vernal pond areas that dry during the summer months. Although collected earlier in Merced, Stanislaus, and Tulare counties, California, it is apparently now restricted to two small populations in the Sacramento Wildlife Refuge south of Willows, Glenn County, California. It appears to be most closely related to the perennial species *Atriplex fruticulosa*.

A distinctive new annual species of *Atriplex* was discovered by the first author in August 1989 in a moist depression approximately 0.5 km southwest of the Sacramento Wildlife Refuge Headquarters, 8 km south of Willows, Glenn Co., California. One other population was later found about 1.5 km northeast of the Sacramento Wildlife Refuge Headquarters. Several searches elsewhere on the Refuge and in surrounding areas did not reveal any other populations. In addition, a study was made of all types and collections of North American annual *Atriplex* in several herbaria, including CAS, DAV, GH, NY, RM, RSA, UC and US. Only three earlier collections of this new species were found and are noted below. Each of these earlier collections was labelled *A. parishii* Watson. Although *A. persistens* plants resemble plants of *A. parishii* in some characteristics, they differ significantly in habit, flowers and fruits. *A. persistens* plants are larger and coarser than *A. parishii* plants and, unlike *A. parishii*, the fruits of *A. persistens* are strongly indurate, dentate on the upper margins, widest above the middle, and are firmly attached to the branches. In *A. parishii* male and female flowers are borne together in axillary glomerules; in *A. persistens* male flowers occur separately in upper leaf axils and in terminal inflorescences.

In repeated searches by the current authors in the areas of the earlier collections, no *A. persistens* plants were found. The required habitat for these species appears to have been destroyed in these areas and may now exist in very few places other than the two sites described above in the Sacramento Wildlife Refuge, suggesting that the species is in need of immediate protection.
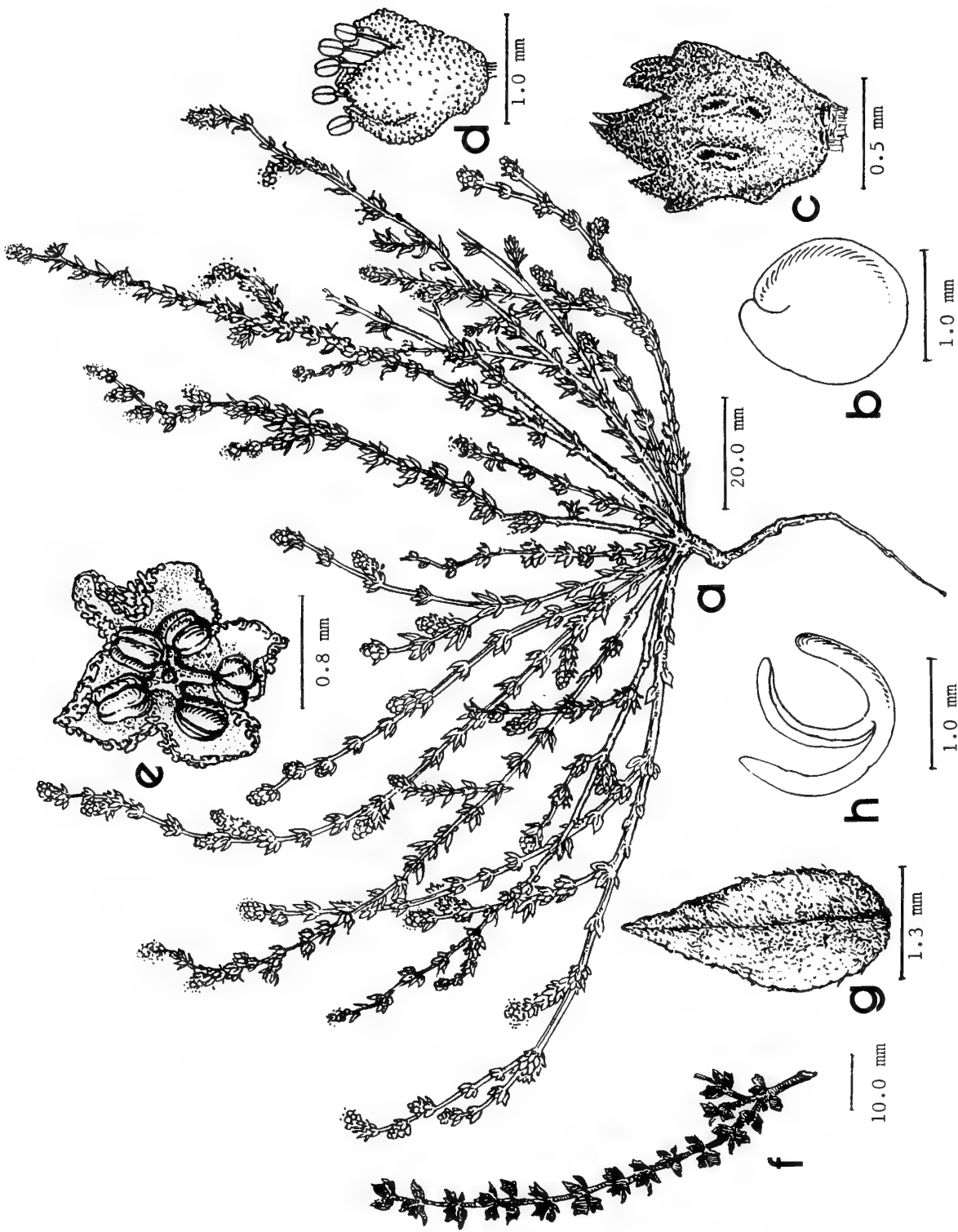
Species Treatment

Atriplex persistens Stutz & Chu, sp. nov. (Fig. 1)—Type: USA, California, Glenn Co., 5 miles S of Willows, ¼ mi SW of Sacramento Wildlife Refuge Headquarters, T18N R3W S9, in a moist depression, 28 Sep 1990, *H. C. Stutz 95413* (holotype, BRY).

Herbae annuae, 10–20 cm altae; caulis erectus vel ascendens, ramis constipatis gracilibus expansis et dense furfuracee farinosis. Folia alterna, ovato usque ovato-lanceata, 2–4 mm longa, 1–3 mm lata, cinereo-virides, apice breviter acuminata, basi cuneata usque fere cordata, integra, sessilia, utrinque dense furfuracee farinosa. Flores monoecii. Staminales flores glomerati ad ramorum apicem axillares, in terminales spicas 0.5–4 cm longos, perianthium fere globosum, 1.5 mm in diam., 5-partitum ad basim, segmentis membranaceis, deltato-ovatis, postice prope apices viridi textura, stamina 5, filamentis filiformibus, antheris circa 0.5 mm longis, pleraque purpurato-rubris. Pistillati flores pleraque solitarii in foliorum oxillis sub staminalis inflorescentiis, bracteolis connatis ad super medio, stigmatibus 2–2.5 mm longis et stylo inconspicuo, fructiferi bracteae ovato-oblongae, leviter compressae, indurescentes ad midium et inferam partem, persistentes, 3–4 mm longae, 2–2.5 mm latae, dense furfuracee farinosae, utrinque 1–2 appendicibus inregularibus tubercularibus. Utriculus lati-ovatus, semen 1.2–1.5 mm in diam., testa membranacea, brunneola, radicula supera.

Annual herbs, 10–20 cm tall. Stems erect or ascending, with crowded, slender, spreading branches and dense, scurfy covering. Leaves alternate, ovate to ovate-lanceolate, 2–4 mm long, 1–3 mm wide, grey-green, short acuminate at apex, cuneate to nearly cordate at base, entire, sessile, densely scurfy on both surfaces, kranz-type venation. Flowers monoecious; staminate glomerules axillary near the tip of branches and in terminal spikes 0.5–4 cm long, perianth nearly globose, ca. 1.5 mm in diameter, 5-parted to middle, segments membranaceous, deltoid-ovate, usually with green tissue on back near apex, stamens 5, with filiform filaments, anthers ca. 0.5 mm long, usually purple-reddish; pistillate flowers usually solitary in axils of leaves below the staminate inflorescence, bracteoles fused to above the middle, stigmas 2–2.5 mm long, style inconspicuous. Fruits broad-ovate, persistent on branches; fruiting bracts sessile, ovate-oblong, slightly compressed, hardened at the middle and below, 3–4 mm

←

Fig. 1. *Atriplex persistens*. a, habit. b, seed. c, fruiting bracts. d, male flower. e, male flower opened to show the stamens. f, dead branch with persistent fruits. g, leaf. h, embryo (drawing by Xia Quan).

long, 2–2.5 mm wide, covered with dense scurf, with 1–2 irregular tuberculate appendages on each surface. Seed 1.2–1.5 mm in diam.; testa membranaceous, red-brown; radicle superior; endosperm copious, irregularly excessive, causing the embryo to sporadically bulge. Flowering period: July–September. Chromosome number, $2n=18$.

PARATYPES: USA, CA: Glenn Co., Sacramento Wildlife Refuge, 5 mi S of Willows, T18N R3W S9, 25 Aug 1989, *H. C. Stutz 95126* (BRY); Sacramento Wildlife Refuge, 5 mi S of Willows, ¼ mi SW of headquarters, *H. C. Stutz 95230* (BRY); Sacramento Wildlife Refuge, 5 mi S of Willows, 1 mi NE of headquarters, T118N R3W S10, 9 Jan 1990, *H. C. Stutz 95231* (BRY); Sacramento Wildlife Refuge, 5 mi S of Willows, 20 May 1990, *S. C. Sanderson* and *G. L. Chu 95290* (BRY); Sacramento Wildlife Refuge, 5 mi S of Willows, ¼ mi SW of headquarters, 16 Aug 1990, *H. C. Stutz 95337* (BRY). Merced Co., Merced Plain, 3 mi SW of Merced, 18 Jun 1926, *J. T. Howell 2036* (CAS). Tulare Co., vernal poolbeds, 0.25 mi N of Avenue 104 on road 124, 280 ft elevation, 3 Aug 1963, *E. C. Twisselmann 8821* (CAS). Stanislaus Co., Carpenter road near San Joaquin River, S of Modesto, 27 Aug 1965, *R. F. Hoover 9519* (CAS, RM).

The closest relative of *A. persistens* appears to be the perennial species *A. fruticulosa* Jepson. Both species have sessile leaves, dentate-margined fruiting bracts and male flowers borne in terminal inflorescences. However, *A. persistens* is clearly distinguished from *A. fruticulosa* not only in being annual instead of perennial but also in having distinctively different fruits. The fruits of *A. persistens* are oblong-ovate, widest above the middle whereas those of *A. fruticulosa* are broadly rhomboid-ovate, widest at the middle. Also the fruits of *A. persistens* are so firmly attached that they persist even on old dead plants.

In the early spring of 1991 and 1993 the basins in which the two known populations of *A. persistens* were found were submerged with 6–12 inches of water. It is not known if this is a regular annual experience nor if it is significant in the survival of *A. persistens*. However, if it is requisite for its success it may help explain its apparent disappearance elsewhere in California. Agricultural practices and the management practices in the wildlife preserves of California would rarely perpetuate such a habitat. If we learn that such a habitat is required by *A. persistens,* hopefully, some of the wildlife preserves could be encouraged to provide areas where it could thrive. Because of the increasing disturbance of critical habitats required for other annual species of *Atriplex* in California it is imperative that their needs be met before they are extinguished. There appears to be some immediate urgency in arranging for adequate habitat for other annual *Atriplex* species in California, including: *A. coulteri* (Moq.) D. Dietr, *A. davidsonii* Standley, *Atriplex joaquiniana* A.

Nelson (*A. spicata* S. Wats.), *A. miniscula* Standley, *A. parishii* S. Wats., *A. tularensis* Coville (it may already be extirpated, e.g., Freas and Murphy 1988), and *A. vallicola* Hoover.

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ANNOUNCEMENT

VI LATIN AMERICAN BOTANICAL CONGRESS, MAR DEL PLATA, ARGENTINA, 2–8 OCTOBER 1994

The VIth Latin American Botanical Congress (VI Congreso Latinoamericano de Botánica) will be held 2–8 October 1994 in Mar del Plata, Argentina. Mar del Plata is located 410 km south of Buenos Aires, on the Atlantic coast of Argentina.

The Congress is sponsored by the Sociedad Argentina de Botánica (SAB) and the Asociación Latinoamericana de Botánica (ALB).

The scientific program will include symposia, poster presentations, "all congress" lectures, and satellite meetings. The official languages of the Congress will be Spanish and Portuguese. Simultaneous English-Spanish translation will be provided, as needed. Papers intended for publication in the Congress proceedings can be submitted in Spanish, Portuguese or English.

The first circular, which includes a preliminary registration form, is now available. For further information, or in order for your name to be added to the mailing list, please contact: Dr. Arturo Martínez, Presidente, Comité Organizador, or Ing. Agr. Renée H. Fortunato, Secretaria Ejecutiva, VI Congreso Latinoamericano de Botánica, Instituto de Recursos Biológicos, INTA, Castelar 1712, Provincia de Buenos Aires, Argentina. (FAX: 54-1-481-2360.)

A NEW SPECIES OF *BROWALLIA* (SOLANACEAE) FROM THE SOUTHWESTERN UNITED STATES AND NORTHWESTERN MEXICO

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ABSTRACT

Browallia eludens is a new short-lived summer annual species from the Canelo Hills, Santa Cruz County, Arizona, and west-central Chihuahua and southeastern Sonora, Mexico. It belongs in Section *Browallia* with three of the four other Central and South American species. They share a small corolla with rounded lobes and an uninflated calyx. **Browallia eludens** is distinguished by its narrow, subsessile leaves, consistently whitish flowers, oversized calyx and larger, distinctively shaped seeds. It occurs primarily in riparian habitats in Madrean Evergreen Woodland in southern Arizona and the northern Sierra Madre Occidental. This is the first report for an indigenous species of the genus *Browallia* from the United States.

RESUMEN

Se describe **Browallia eludens**, sp. nov., anual con ciclo corto en verano, de Canelo Hills, Santa Cruz County, Arizona, y del centro-occidente de Chihuahua y sureste de Sonora, México. Pertenece a la sección *Browallia* junto con otras tres de las cuatro especies de Centro y Sudamérica. Comparten una pequeña corola con lóbulos redondeados y cáliz no inflado. **Browallia eludens** se distingue por sus hojas estrechas, subsésiles, flores consistentemente blanquecinas, cáliz agrandado y semillas más grandes con forma distinta. Habita principalmente habitats riparios del bosque de pino y pino-encino del sureste de Arizona y del norte de la Sierra Madre Occidental. Este es el reporte primero del genero *Browallia,* de los Estados Unidos.

While on a botanical outing to the Canelo Hills of southern Arizona in August 1990, we discovered an interesting plant that could not be easily assigned to family. In the next year several additional collections of the plant from west-central Chihuahua (Laferriere 1991) and southeastern Sonora, Mexico, were brought to our attention. Further study revealed that this species belonged to the genus *Browallia,* a small group of neotropical annuals in the Solanaceae. Study of known material of *Browallia* showed these populations to be a new species.

SPECIES TREATMENT

Browallia eludens Van Devender & Jenkins, sp. nov. (Fig. 1). — TYPE: USA, Arizona, Santa Cruz Co., ca. 1.6 km N of Canelo Pass in Western Canyon, Canelo Hills, Coronado National Forest, T22S
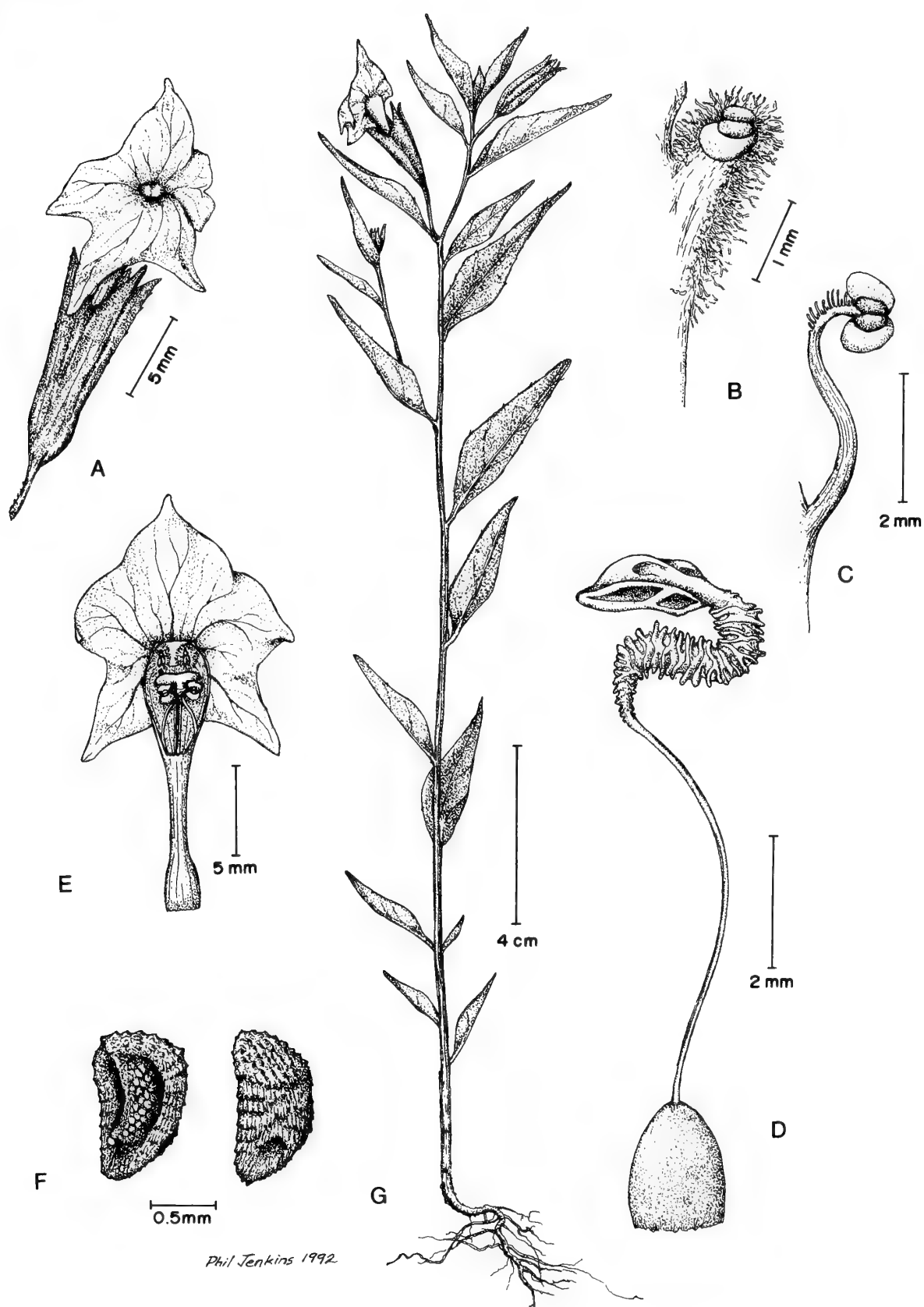
FIG. 1.   *Browallia eludens.* A, flower. B, upper stamen. C, lower stamen. D, ovary, style and stigma. E, top view of flower with section of corolla removed to show position of stamens and stigma. F, seed: ventral surface with keel and hilum (left); dorsal surface (right). G, entire plant.

R18E S19, NW¼, 1600 m, 25 Aug 1990, *Van Devender 90-421* (holotype, ARIZ; isotypes; GH, MO, UC, US).

Herba annua, erecta, 8–30 cm alta, plerumque non ramosa. Folia alterna, integra, subsessilia vel brevi-petiolata, rhombici-lanceolata pro parte maxima, lineari-lanceolata superne, usque ad 4 cm longa et 1 cm lata, marginibus brevibus hispidi-ciliatis. Florae solitariae, axillares; pedicelli usque ad 15 mm longi. Calyx 8–15 mm longus, 5-lobatus et valde 5-plicatus, lobis leviter inaequalibus, acutis, ad 6 mm longis. Corolla zygomorpha, cremea vel flavida, hypocrateri-morpha, limbo 5-lobato, 6–12 mm lato, tubo et fauce 10–17 mm longo, vix exserto calyce et protuberatione adaxiale ad faucem. Stamina 4, didinama; antherae paris superi utraque ferens thecam abortivam unicam; filamenta staminum superiorum applanata, marginibus dense lanati-pubescentibus; filamenta staminum inferiorum angusta, semel geniculata et pubescenta solum superne. Ovarium viridum, glabrum; stylus semel geniculatus superne; stigma late 2-lobatum, tegens ambas antheras staminum inferiorum. Capsula bivalvis, omnino inclusa calyce accrescenti. Semina circa 1.5 mm longa, numerosa, brunnea vel ligno-brunnea, minute reticulata et papillata.

Erect annuals 8–30 cm tall, typically unbranched; stems minutely pubescent in lines with short, incurved hairs. Leaves alternate, entire, subsessile or short-petiolate, to 4 cm long and 1 cm wide, prevailingly rhombic-lanceolate, the upper becoming linear-lanceolate; blade short hispid-ciliate along the margins and sometimes sparsely on veins below. Flowers solitary, axillary, on pedicels to about 15 mm long, only 1 or 2 opening simultaneously. Calyx 8–15 mm long, 5-lobed, strongly plicate along midrib of each lobe, hispid-ciliate on margins and plicae; lobes slightly unequal, acute, to 6 mm long. Corolla zygomorphic, cream-colored (pale yellow in age), salverform, the limb 6–12 mm across, declined obliquely on the tube, 5-lobed with tips reflexed; tube including throat 10–17 mm long, scarcely exserted from the calyx, lightly glandular-puberulent outside; throat ventricose adaxially, the swelling formed by the cluster of stigma and anthers of the 2 lower stamens. Stamens 4, didynamous; anthers of upper pair each with one abortive theca, the filaments flattened and expanded, densely ciliate with long, woolly and somewhat viscid hairs, the apices of the filaments curved downward and closing the mouth of the corolla, sometimes exposing the abortive thecae; anthers of lower pair each with 2 fertile thecae, the filaments narrower, once-geniculate and pilose only near apices. Ovary glabrous, green, 2-celled with axile placentation; style once-geniculate near apex and strongly convoluted the length of bend; stigma a broadly 2-lobed expanded cap, the ventral surface bearing 2 pockets which enfold the anthers of lower stamens. Fruit a 2-valved

septicidal capsule included in the accrescent calyx; seeds about 1.5 mm long, numerous, tan or dark brown at maturity, excavated on the inner (concave) surface except for a central keel, minutely reticulate; outer (convex) surface rounded and minutely papillate.

PARATYPES: USA, Arizona, Santa Cruz Co., ca. 1.6 km N of Canelo Pass in Western Canyon, Coronado National Forest, 1600 m, 11 Aug 1990, *Van Devender 90-367* (ASU); Western Canyon, T22S R18E S18, SW¼, 1600 m, 19 Aug 1990, *Jenkins 90-91* (ARIZ, F). MEXICO, Chihuahua, ridge W of Moris, 28°08′N, 108°35′W, 1500 m, 19 Aug 1989, *Martin & Jenkins 89-313* (ARIZ); km 89 on road from Basaseachic to San Juanito, 28°09′N, 108°9.8′W, 2100 m, 15 Aug 1989, *Martin, Rondeau & Jenkins 89-184* (ARIZ); Municipio Temosachic, 1 km N of Nabogame, 28°30′N, 108°30′W, 1800 m, 29 Aug 1987, *Laferriere 1003* (NMC, VDB); 3 km N of Nabogame, 27 Jul 1988, *Laferriere 1562* (TEX, VDB); Nabogame, 8 Aug 1988, *Laferriere 1629* (ARIZ, MEXU, VDB); Rancho Byerly, Sierra Charuco, 1350–1700 m, summer 1946, *Langille 71* (ARIZ). Sonora, "El Rayo" on the way to Milpillas, 27°15′20″N, 108°37′50″W, 1430 m, 18 Aug 1991, *Martin & Jenkins 91-84* (ARIZ).

Comparison with other species. Unlike most other Solanaceae, *Browallia* has a zygomorphic corolla and four didynamous stamens. The anthers of the upper pair each bear one abortive and one fertile theca. In this genus alone the upper anthers curve downward, elevating the flattened, densely ciliate filaments that effectively close the very small mouth of the corolla (D'Arcy 1978).

Although 27 species of *Browallia* have been described, only four are currently recognized (W. G. D'Arcy personal communication 1991). *Browallia eludens* differs from these in a number of morphological characters. It is typically unbranched with consistently narrow, subsessile leaves. The other species are usually much branched with primarily ovate, petiolate leaves.

Browallia eludens has whitish flowers turning pale yellow with age and the corolla tube is scarcely exserted from the comparatively oversized calyx. The others, especially *B. americana,* are noted for variable flower colors, typically some shade of blue, but ranging from white to purple. A white or yellow eye is often apparent in the throat. The corolla tube is well exserted in these species, due to the relatively smaller calyx.

The pollen morphology of *Browallia eludens* differs from that of *B. americana* (Gentry 1979) and the Solanaceae in general (Punt and Monna-Brands 1980) which are typically tricolporate and striate. In a scanning electron microscope (SEM) image, the unacetolyzed pollen grain of *Browallia eludens* appears inaperturate with a scabrate surface (Fig. 2). Pollen were examined from the upper and lower anthers of 10 flowers. Grains were teased from the anthers,
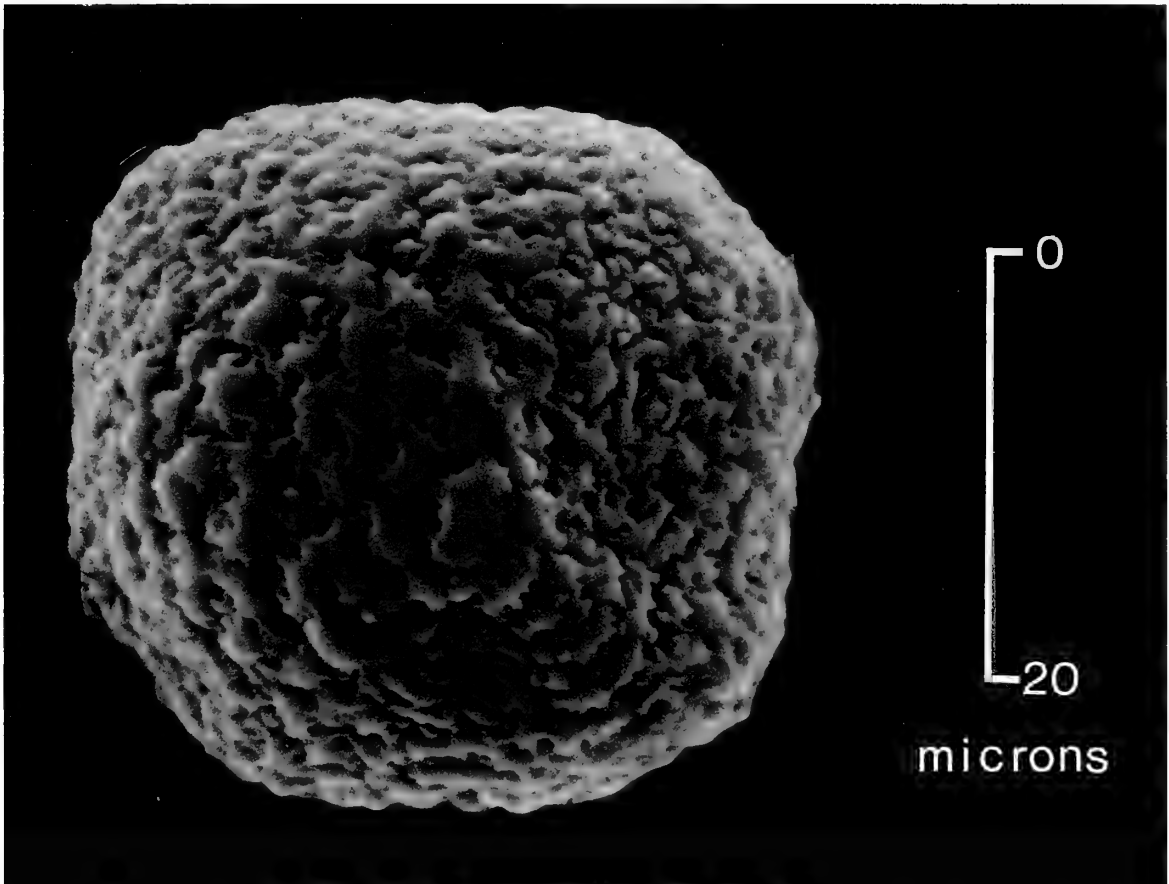
Fig. 2. Scanning electron microscope photo of an unacetolyzed pollen grain of *B. eludens* from Canelo Hills, Arizona. Note scabrate surface and apparent lack of apertures.

mounted in glycerin jelly, and stained with basic fuchsin for quick examination. Pollen were 37 × 40 μm in size. Some grains appeared to be striate with 3–6 colpae (commonly 4 or 5) with a small polar index (PAI = 0.90; Fig. 3). The dense ektexinous elements in the colpae contribute to the inaperturate appearance of the pollen grain under SEM. Grains from upper and lower anthers may mature at different rates because some appeared thin walled and striate while others appeared thicker walled and scabrate. Acetolysis was performed three times on separate samples. Pollen fragments were found after each extraction attempt, but entire pollen grains were never recovered. Within three months pollen in the glycerin mounts had appreciably disintegrated suggesting that the exine is very fragile.

The seeds of *Browallia eludens* (typically 1.5 mm long) are larger than those of the other species, which seldom reach 1 mm. They are excavated on the inner side and rounded on the back, resembling most closely seeds of *B. acutiloba*. The other species have strongly prismatic seeds. Only *B. eludens* has seeds which bear a prominent longitudinal keel on the concave (ventral) side.

It is difficult to determine, with the information available to us, the closest relative of *B. eludens*. The small flowers with shallow,
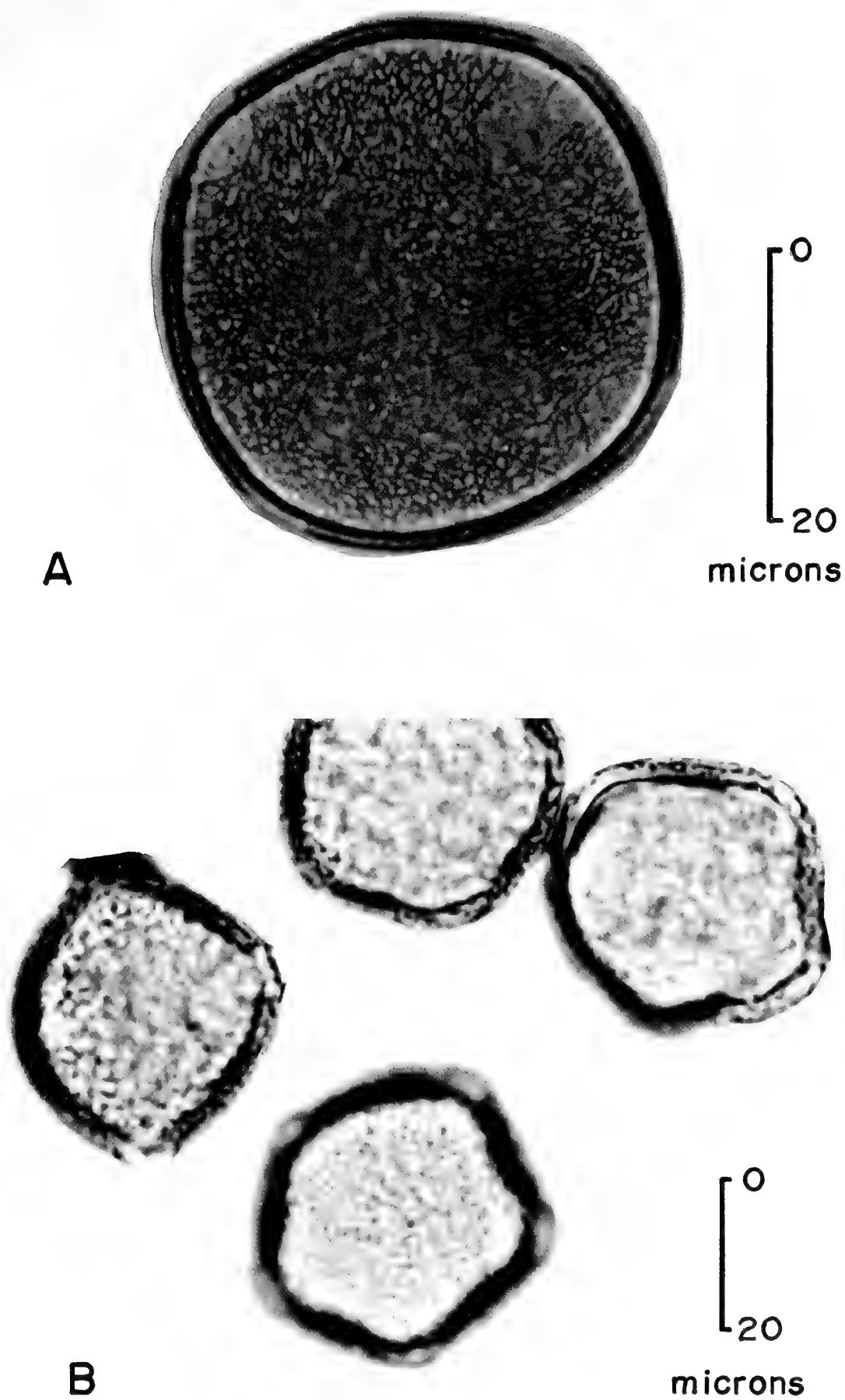
FIG. 3.   Light micrographs of pollen grains of *B. eludens*. A, 4-colpate grain with striate appearance. B, 4- and 5-colpate grains with scabrate surface.
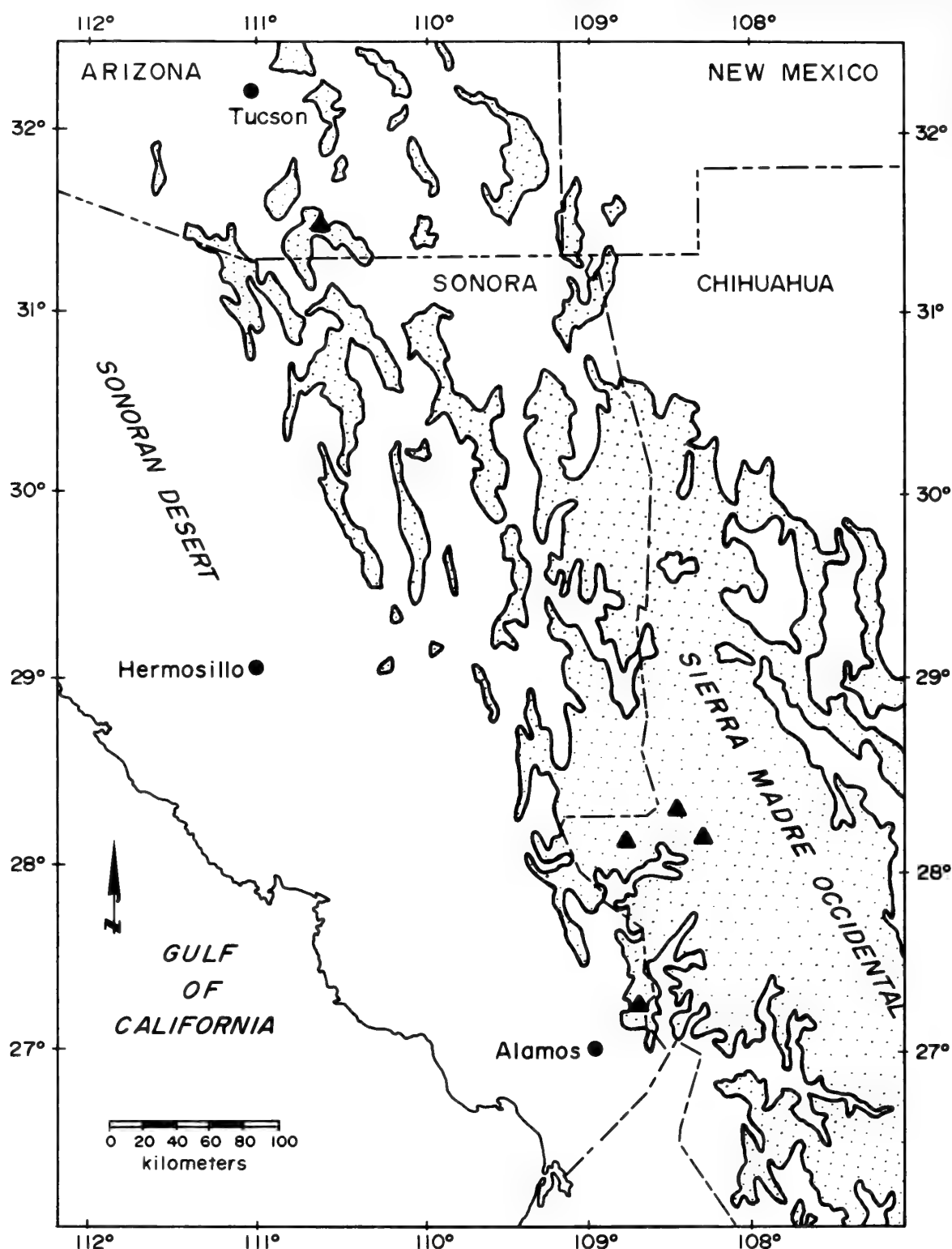
FIG. 4. Distribution map of *Browallia eludens*. Triangles = collection localities; stippled area = Sierra Madrean Woodland and Forest, after Brown and Lowe (1980).

rounded corolla lobes and uninflated calyx would indicate it belongs in Sect. *Browallia,* which includes the most northern of the species, *B. americana,* and the closely related *B. viscosa,* formerly regarded as a glandular form of *B. americana* (D'Arcy 1973). Sagástegui Alva and Díos Carranza (1980) described *B. acutiloba* from the lowlands

of northern Peru, suggesting it was most similar to *B. speciosa.* However, the large flowers, deeply pointed corolla lobes and inflated calyx of *B. speciosa* are so unusual that D'Arcy (1973) referred it to a separate section, Sect. *Leiogyne.* We believe that *B. acutiloba* belongs more properly in Sect. *Browallia* because it shares the corolla and calyx features of species placed in that section.

Distribution, habitat and phenology. Browallia eludens is currently known from disjunct populations in southeastern Arizona, west-central Chihuahua, and southeastern Sonora, Mexico, from 31.5° to 27.2°N latitude (Fig. 4). The localities vary from 1400–2100 m where the dominant species are various evergreen oaks and Mexican pines characteristic of Madrean Evergreen Woodland (Brown 1982). At the type locality in the Canelo Hills the vegetation is oak woodland dominated by Emory oak (*Quercus emoryi*) with scattered alligator bark juniper (*Juniperus deppeana*). In Mexico *B. eludens* occurs in oak and pine-oak woodland and, at the highest known elevation, in transitional pine forest. At the lower or drier sites Chihuahua oak (*Q. chihuahuensis*) is often a dominant. It is variously associated with other evergreen oaks (*Q. cocolobifolia, Q. crassifolia, Q. durifolia, Q. oblongifolia, Q. viminea*) and madrone (*Arbutus arizonica, A. xalapensis*). At higher elevations oak woodland is replaced by pine-oak woodland. Some of the same oaks intermingle with pines (*Pinus arizonica, P. durangensis, P. oocarpa*). At 2100 m pine-oak woodland gives way to pine forest dominated by Durango pine (*P. durangensis*) mixed with Arizona pine (*P. arizonica*). Oaks, particularly *Q. crassifolia,* are present, but in much fewer numbers than pines (P. S. Martin and J. E. Laferriere personal communication 1991).

Browallia eludens grows on soils derived from rhyolitic or andesitic volcanic rocks. In Arizona the plants were found only on wet soils in the relatively flat (<30% slope) flood zone of an intermittent stream. Steady stream flow with occasional flooding was evident in August 1990, the year of collection, due to exceptional summer rains. A nearby weather station at Canelo (ca. 5 km NE; 1527 m) recorded 320 mm precipitation for July and August, more than 100 mm above normal (NOAA 1990). In contrast, *B. eludens* was not found in the summer of 1991 with scanty precipitation. Although the Canelo station was no longer active, data from the nearest stations at Sierra Vista (ca. 25 km east; 1402 m) and Patagonia (ca. 20 km west; 1277 m) recorded only 132–142 mm precipitation for July and August (State Climatological Laboratory personal communication 1991). Although these stations were in somewhat lower, and therefore drier, areas the decrease in precipitation is significant.

In Mexico *Browallia eludens* was found in mesic, but not strictly riparian, situations including a wet meadow and a dripping, andesitic rock outcrop, as well as a stream floodplain. Summer rain is more

predictable in the Sierra Madre than in Arizona with more extended periods of moist soil.

To date, *B. eludens* has only been collected in August. The plants apparently senesce with the onset of drier conditions during September.

DISCUSSION

The discovery of *B. eludens* is interesting in several respects. It is widely disjunct from any of its relatives, which are native to southern Mexico, Central and South America. *Browallia americana,* the most widespread species, has long been cultivated in tropical and subtropical America where it often escapes to flourish in disturbed areas (Hunziker 1979). It is common in coffee plantations of central Veracruz (Nee 1986) and is known from as far north as Tepic, Nayarit (*E. Palmer, 2026,* New York).

Browallia eludens is apparently confined to more temperate elevations (1400 to 2100 m) where summers are relatively cool and freezing temperatures routinely occur in winter. Its lower elevational limits appear to be set by sporadic summer precipitation coupled with high temperatures and low humidity, and its upper limits perhaps by cool soil temperatures. Its short, ephemeral life cycle probably permits the species to occupy a niche in woodland during the warm, wet summer, existing as seed during winter. We do not know germination requirements, although we speculate that warm, wet soils are necessary and that the seeds remain dormant for long periods awaiting adequate summer rainfall.

Browallia eludens appears to be tracking the boundaries of Madrean Evergreen Woodland, a mild winter–wet summer woodland centered in the Sierra Madre Occidental. A suite of other tropical and subtropical plants including coralbean (*Erythrina flabelliformis*), mala mujer (*Cnidoscolus angustidens*) and manihot (*Manihot angustiloba*) reach their northern limits in this woodland which extends north to the mountains of southeastern Arizona (northwest to Yavapai County) and into southwestern New Mexico and Trans-Pecos Texas (Brown 1982). In these outlying areas we expect *B. eludens* to occur only sporadically, and in canyons where water is concentrated. In the Sierra Madre with dependable summer rainfall *B. eludens* undoubtedly occurs more frequently and is more widespread.

We were surprised to find a new species, much less one in a tropical genus, in such a well-botanized area. Considering the hundreds of plants in the two Canelo Hills populations, it is doubtful that *B. eludens* has only recently migrated north into Arizona. More likely, the species has been overlooked for several reasons due to its diminutive size, unobtrusive appearance, short life cycle, sporadic occurrence only in wet summers and limited distribution in canyon

riparian woodland habitats. After searching in vain for *Browallia* at the type locality in 1991, its ephemeral and illusive nature suggested to us the epithet, "*eludens.*"

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FACTORS INFLUENCING POSTFIRE SPROUTING VIGOR IN THE CHAPARRAL SHRUB *ADENOSTOMA FASCICULATUM*

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Abstract

Several indices characterizing prefire size and structure of *Adenostoma fasciculatum* shrubs were measured in a chaparral stand slated for an experimental burn. Burl concentrations of total nonstructural carbohydrates (TNC) were also assessed. Following the fire, aboveground biomass production during the first postfire year was determined. In addition, a shading experiment was implemented after the fire to assess the contribution of current photosynthesis of sprouts to postfire sprouting vigor.

Postfire biomass production was positively correlated with prefire shrub size, but negatively correlated with prefire dead stem area and percent dead stem area. Burl TNC concentrations showed no patterns with respect to prefire shrub size, the percent dead stem area, or postfire sprouting vigor. Reducing incident sunlight with shadecloth resulted in significant reductions in postfire biomass production. Our results suggest that stands of *A. fasciculatum* having high components of standing dead biomass sprout less vigorously after fire.

Substantial biomass levels and prolonged seasonal drought combine to ensure that fire plays an important role in the shrub-dominated chaparral of California. Although the "natural," pre-European fire frequency in this vegetation is the subject of much debate, it is often said that stands of chaparral burned on the average of every 20–40 years prior to modern fire suppression practices (e.g., Philpot 1977; Minnich and Howard 1984). Some evidence indicates that fire suppression practices may have resulted in fewer, but larger and more destructive fires in recent decades (Minnich 1983), because fire suppression may have led to a preponderance of old stands of chaparral with higher proportions of dead fuels. Such old stands might be expected to burn more destructively in a wildfire than younger stands with less dead fuel accumulation. In any case, the current juxtaposition of chaparral with the ever-encroaching urban areas of southern California has necessitated the adoption of prescribed burning by land management agencies to reduce fuel loads and fire hazard. Certainly the need has never been greater for basic information on how chaparral species respond to fire.

Many chaparral shrub species sprout vigorously after fire, a characteristic that likely confers an enormous advantage to sprouting

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species compared to nonsprouting, obligate seeding species. Sprouting shrubs have mature root systems, with their carbohydrate and nutrient reserves, as well as greater access to soil water and nutrients compared to seedlings. Sprouting shrubs suffer little of the drought-induced mortality that is common among postfire seedlings (Kummerow et al. 1985).

Despite the importance of postfire sprouting in the California chaparral, little is known about the controls of sprouting success and vigor. In a study of *Adenostoma fasciculatum* H. & A. (Rosaceae) (chamise) (nomenclature follows Munz 1974), a widespread sprouting shrub species in the California chaparral, Jones and Laude (1960) concluded that root, shoot, and root crown (burl) total nonstructural carbohydrate (TNC) levels were influential in chamise growth rates after mechanical cutting, since little fall and winter growth (when TNC levels were low) was observed even when temperature and moisture conditions were favorable. However, Radosevich and Conard (1980) have shown that the lower initial growth rates of chamise shrubs burned when TNC levels were low did not result in shorter shrubs after two seasons of growth; hence, current photosynthesis of sprouting shoots, and not belowground TNC levels only, may also influence postfire sprouting vigor.

A major remaining deficit of information regarding sprouting is whether prefire shrub condition, as expressed by shrub size and the amount of standing dead biomass, influences postfire sprouting vigor. If land managers using prescribed burning are to contend with an increasing proportion of older stands of chaparral with higher levels of standing dead biomass, then it will become increasingly important to understand whether shrubs in different prefire condition respond to fire differently.

We investigated three aspects of the response of sprouting *Adenostoma fasciculatum* to fire. First, we were interested in determining whether prefire shrub condition, as assessed by shrub size and the amount of standing dead fuels in the shrub, influenced postfire ⁻prouting vigor. We therefore examined the relationships between several indices of prefire shrub size and structure, and postfire sprouting vigor. Second, we were interested in exploring further the influence of prefire shrub storage carbohydrate (TNC) levels on postfire sprouting vigor, and how such TNC levels might differ in shrubs of different prefire condition. Third, we evaluated the contribution of current photosynthesis of sprouting shoots to postfire sprouting vigor in a shading experiment.

Materials and Methods

Structural characteristics were recorded for 73 *Adenostoma fasciculatum* (chamise) shrubs growing in a 54-year old (i.e., 54 years

since the previous fire) mixed chaparral community scheduled for an experimental burn in the autumn of 1982. The stand was located on a north-facing slope (1400 m elevation) at the Sky Oaks Biological Field Station in northeastern San Diego County, California. The total size of the study area was about 0.25 ha (50 × 50 m). Chamise shrubs in this stand could be found in a variety of sizes and with a variety of levels of standing dead biomass. Co-occurring shrub species included *Ceanothus greggii, Quercus dumosa,* and *Adenostoma sparsifolium.*

Chamise shrubs were selected by establishing transects on the study slope at 10 m intervals, and points along the transect were chosen at random. Data were collected from the chamise shrub nearest to the random point. For all 73 chamise shrubs the following data were taken: (1) length and width measurements of each burl (enough soil was removed from around the burl so that the true shape could be ascertained, since burls were often irregular in shape; the longest axis was chosen as the length, and the axis perpendicular to the length was chosen as the width); (2) number and diameter of all live and dead stems at 10 cm height above the burl; and (3) canopy length and width measurements, using the same method described above for measuring burl dimensions.

Burl length and width measurements were used to calculate burl area, an index of burl size. Burl volume was not measured since its determination would require destructive sampling. Similarly, canopy length and width measurements were used to calculate a rough estimate of canopy area, an index of shrub size. Stem diameters were used to calculate stem areas, which were then summed across all stems to obtain total live and dead stem areas for each shrub.

After collection of shrub structural data, a small sample of woody tissue was removed from each burl for total nonstructural carbohydrate (TNC) analysis. Samples (1–2 g dry weight) were removed by drilling into the burl approximately 1 cm deep and collecting the drill shavings. Since burls were composed of both functional and nonfunctional material, burl samples were consistently taken near the base of live stems to obtain samples from functional (i.e., nondecaying) woody tissue. More thorough characterization of burl TNC status would have entailed greater potential perturbation to the shrubs' postfire sprouting. Sampling was completed during a six week period (early October to mid November), and tissue was collected at whatever time of day a particular shrub was visited. Samples were dried in a forced draft oven (57°C) for 48 hr, placed in a sealed vial, and stored until analyzed. Total nonstructural carbohydrates were quantified using a Technicon autoanalyzer following the procedure of Smith (1969).

Because of various weather factors, the scheduled experimental burn was postponed until January 1984, approximately one year

after the data above were collected. Although changes in burl TNC concentrations probably occurred during this interval, it is likely that TNC relationships among the shrubs of various sizes and conditions remained unchanged. Certainly shrub structural characteristics did not change ostensibly during this time interval, and any trends in relative shrub condition would likely occur at a time scale longer than one year in this 54-year-old stand. We cannot, however, determine whether or not significant changes in relative shrub condition occurred during the delay.

An off-season burn was deemed necessary to reduce fire hazards, and the burn was carried out under cool (10–20°C) and cloudy conditions. The burn was, however, complete over the 0.25 ha study area. Shrub growth is negligible at this elevation in the winter, so shrubs had not yet invested in any new growth.

All shrubs were numbered and tagged with stainless steel tape before the fire. In October 1984, after one postfire growing season, total aboveground sprout biomass (excluding the charred remains of branches) of each shrub was harvested, dried (40–50°C for 5–7 days), and weighed.

In May 1984, prior to any postfire sprouting, each of 17 shrubs (randomly chosen from among the original sample of 73 shrubs) was enclosed within an approximately 50 × 50 cm frame (exact shape depended on burl dimensions) onto which shadecloth was fastened to form a canopy over each burl, and which enclosed the burl on three sides. Shadecloth was of a standard nursery variety affording approximately 84% shade (16% transmittance). The east side of these shadecloth "tents" was left open so all burls would receive full sunlight for a part of the morning. In this way, peak irradiance was not inhibited to an extent that would cause the shoots to etiolate. Total postfire aboveground sprout biomass of the shaded individuals was also determined in October 1984.

Of the 73 shrubs described before the experimental burn, 15 were cut by fire crews a few days before the fire, and two shrubs did not survive the fire. The final sample consisted of 56 shrubs, 17 of which were enclosed in shadecloth tents (hereafter referred to as the "shaded shrubs"), while 39 were assigned to be the reference plants (hereafter referred to as the "unshaded shrubs").

Prior to calculating correlation coefficients, dependent variables (production and production per unit shrub size) were plotted against each measure of shrub structure to determine whether relationships were linear or non-linear and to evaluate subjectively the strength of the relationship. If statistically significant correlation coefficients were based on a few outliers, the "significance" of the relationship was not accepted. All relationships that were determined to be significant appeared to be linear.

One measure of shrub structure, percent live stem area, was arc-

Table 1. Means and Ranges of Several Variables Measured for Unshaded and Shaded *Adenostoma fasciculatum* Shrubs before a Controlled Burn, Plus the Mean and Range for Aboveground Net Postfire Biomass Production of These Shrubs during the First Postfire Growing Season (May to October). No significant differences were found between unshaded and shaded shrubs for any of the variables except postfire biomass production (t-test, $\alpha = 0.05$).

		Unshaded shrubs (n = 39)	Shaded shrubs (n = 17)
Burl area (cm²)	Mean	833.6	609.2
	Range	(143–2805)	(150–1748)
Canopy area (cm²)	Mean	18,289	17,729
	Range	(3200–51,750)	(440–47,385)
Live stem area (cm²)	Mean	38.8	40.8
	Range	(5–109)	(7–130)
Dead stem area (cm²)	Mean	14.3	12.5
	Range	(0–41)	(0–73)
Total stem area (cm²)	Mean	53.1	53.3
	Range	(12–129)	(7–203)
Live stem area (%)	Mean	70.5	80.2
	Range	(30–100)	(49–100)
Live stems (#)	Mean	9.2	10.7
	Range	(1–22)	(2–24)
Burl TNC conc. (mg TNC/g dry wt.)	Mean	76.1	77.6
	Range	(49–107)	(57–105)
Production (g dry wt.)	Mean	362.0	161.1
	Range	(0–873)	(7–423)

sine-square root transformed (Neter et al. 1985), which, based upon inspection of residual plots, appeared to stabilize the variance. Homogeneity of variance was assessed for all other variables, based upon inspection of residual plots.

Stepwise multiple regression was used as a tool to ascertain the most influential variables in an effort to construct models predicting shrub biomass production and relative biomass production as a function of prefire shrub structure. In all cases, adding more independent variables to the model did not result in adequate improvements over the single variable models. Since coefficients of determination were never high enough to yield a solidly predictive relationship, the effort to construct "best fit" models was abandoned.

Results

Means and ranges of all prefire indices are shown in Table 1 for both shaded and unshaded shrubs. No significant differences were found between shaded and unshaded shrubs for any prefire (and pretreatment) index (t-test, $\alpha = 0.05$).

Unshaded shrubs. Postfire aboveground sprout biomass production in unshaded chamise shrubs was significantly associated with several indices of prefire shrub size, specifically the number of live stems, burl area, canopy area, live stem area, total stem area, and the (arcsine-square root transformed) percent live stem area (Table 2). Live stem area produced the highest correlation coefficient with postfire biomass production ($r = 0.77$, $P < 0.001$; Table 2). Postfire biomass production was not associated with prefire dead stem area nor with prefire burl TNC concentration.

Although biomass production was significantly correlated with burl area and canopy area, these two measures of prefire shrub size were not significantly correlated with one another. Burl area was positively correlated with live ($r = 0.55$, $P < 0.0003$) and total stem area ($r = 0.67$, $P < 0.0001$). Canopy area was significantly associated with live ($r = 0.54$, $P < 0.0007$) and total stem area ($r = 0.48$, $P < 0.003$), and with the number of live stems ($r = 0.38$, $P < 0.023$). Neither burl area nor canopy area was significantly associated with the proportion of live stem area, indicating that shrub size was not related to the proportion of live (or dead) stem area.

Prefire burl TNC concentrations showed no significant correlations with any indices of prefire shrub size or structure, nor with postfire biomass production.

In order to control for shrub size in considerations of postfire sprouting vigor, we derived two measures of postfire unit production by dividing biomass production by prefire burl area and prefire canopy area (Table 2). Unlike simple production, biomass production/burl unit area was significantly associated with only two measures of prefire shrub structure—negatively correlated with dead stem area and positively correlated with (arcsine-square root transformed) percentage live stem area (Table 2). Interestingly, biomass production/burl unit area was not correlated with live stem area, which had the best association with simple production, whereas simple production was not correlated with dead stem area, which had the best association with biomass production/burl unit area. Biomass production/canopy unit area was positively associated with prefire live stem area, as well as with prefire burl area and the number of live stems.

Shaded shrubs. No significant correlations were found between postfire production and any prefire shrub index for shaded shrubs, perhaps in part because the sample size is smaller ($n = 17$, compared with $n = 39$ for the unshaded shrubs).

Aboveground net biomass production in the season following the experimental burn was significantly greater for the unshaded shrubs compared with the shaded shrubs (t-test, $P < 0.0001$) (Table 1). The unshaded shrub average biomass production was 2.2 times greater

TABLE 2. CORRELATION COEFFICIENTS OBTAINED FROM CORRELATING POSTFIRE ABOVEGROUND BIOMASS PRODUCTION AND PRODUCTION PER UNIT PREFIRE SHRUB SIZE (PRODUCTION PER UNIT BURL AREA AND PRODUCTION PER UNIT CANOPY AREA) WITH SHRUB PARAMETERS MEASURED BEFORE THE FIRE (TOTAL NONSTRUCTURAL CARBOHYDRATE CONCENTRATION, OR TNC, THE NUMBER OF LIVE STEMS, BURL AREA, CANOPY AREA, LIVE STEM AREA, DEAD STEM AREA, TOTAL STEM AREA, AND THE PERCENT LIVE STEM AREA). Percentage live stem area data were transformed (arcsine-square root) before calculating correlation coefficients. "ns" = non-significant; "*" = variables collinear.

	TNC	# live stems	Burl area	Canopy area	Live stem area	Dead stem area	Total stem area	% live stem area
Production	ns	0.69 $P < 0.001$	0.43 $P < 0.006$	0.45 $P < 0.005$	0.77 $P < 0.001$	ns	0.64 $P < 0.001$	0.40 $P < 0.011$
Production/burl area	ns	ns	*	ns	ns	−0.60 $P < 0.001$	ns	0.49 $P < 0.002$
Production/canopy area	ns	0.50 $P < 0.002$	0.41 $P < 0.012$	*	0.36 $P < 0.032$	ns	ns	ns

than the average biomass production of the shaded shrubs for the postfire growing season of May to October 1984. Biomass production/burl area was also significantly greater for the unshaded compared to shaded shrubs (P < 0.014).

DISCUSSION

In this 55-year-old stand (i.e., 55 years since the previous fire), *Quercus dumosa* and *Ceanothus greggii* constituted the majority of the cover and the stand appeared to be vigorous in that most shrubs were tall and leaf area index, although not measured, appeared to be high. Many chamise shrubs had high components of standing dead biomass, however, and over 50% of the total stem area was dead in some individuals. High competition for light on this north-facing slope may have induced much of this stem mortality in the lower, shaded branches. It should be noted, however, that the time elapsed since the last fire approached that sometimes associated with stand senescence in the literature (e.g., Hanes 1971; Rundel and Parsons 1979, 1980).

Chamise shrubs that were large before the experimental fire, as estimated by burl or canopy size, tended to produce more biomass after the fire. Similar results have been observed for chamise growing in the foothills of the Sierra Nevada (Stohlgren et al. 1984). This result may appear somewhat trivial, but nevertheless has important ramifications. A shrub that attains some modicum of canopy dominance before a fire is likely to maintain that dominance after the fire, potentially enabling such individuals to remain large and dominant across multiple fire cycles. However, Keeley (1973) observed that large chamise shrubs sprouted less frequently after wildfires, perhaps due to heart rot (cf. Stohlgren et al. 1984). Whether similar relationships between shrub size and sprouting exist for other species of sprouting shrubs would be interesting to ascertain.

Shrubs having high dead stem area or high proportions of dead stem area (i.e., low percentage live stem area) before the fire tended to produce less sprouting biomass per unit prefire shrub size (as measured by burl area) in the first postfire season. If a high dead biomass component in individual shrubs indicates shrub senescence, as a high standing dead biomass component in stands might indicate stand senescence (e.g., Hanes 1971), then our data show that such "senescing" shrubs tend to recover less vigorously after the fire than shrubs with higher live biomass components. Alternatively, a large dead biomass component in a shrub could simply indicate that it has been weakened by competition. Regardless of the cause, a large prefire dead biomass component indicates a weakened state that is significantly associated with diminished postfire production.

The full range in values of percent live (or dead) stem area was

distributed among shrubs of all sizes, as there was no significant association between proportion of live stem area and burl or canopy area. The observed influence of the proportion of dead stem area on postfire unit production therefore appears to be size independent.

Increased bud mortality during the fire (and the consequent lower postfire sprout production) in shrubs with a high prefire dead biomass component is possible, but seems unlikely given the cool conditions of the fire and the low shrub mortality.

Burl TNC concentrations, which were intended as an index of burl energy reserves, showed no pattern with respect to shrub size, the proportion of dead stem area, or postfire sprouting vigor. Other studies have shown that energy reserves are important in postfire sprouting in chamise (e.g., Jones and Laude 1960; Radosevich and Conard 1980), as well as in *Populus tremuloides* (Shier 1976). We propose four hypotheses for the lack of correlation in our data between postfire sprouting vigor and burl TNC concentrations. First, we had hoped that sampling burl tissue before the fire would provide a tractable index of shrub TNC levels with a minimum of perturbation of the shrubs' postfire sprouting performance. However, the burl may not be an important storage organ. The roots of *Adenostoma fasciculatum* have been shown to contain the greatest concentrations of starch (Jones and Laude 1960). The burl may function largely as a sprouting organ providing protection from the fire for the latent buds (Carrodus and Blake 1970; James 1984; Moreno and Oechel 1991; but compare Mullette and Bamber 1978). Second, shrub TNC levels fluctuate seasonally (Jones and Laude 1960; Shaver 1981). Our burl tissue samples were collected in the autumn when the carbohydrate reserves in chamise may not be replenished from expenditures in spring and summer growth. Perhaps differences in TNC levels among shrubs with differing levels of postfire sprouting are obscured at this time. Third, relationships between burl TNC and shrub structure among the sampled shrubs may have changed during the one year delay between sampling and burning. Fourth, reserve carbohydrates are probably heterogeneously distributed in the burl (James 1984), so single small samples of burl tissue have a low probability of representing the carbohydrate status of the burl. Whatever the reason, the results from our TNC data are inconclusive.

Energy reserves are only one factor which could potentially contribute to postfire sprout production. Results from the shading experiment demonstrate that current photosynthesis of sprouting shoots contributes significantly to postfire aboveground biomass production. While our burl TNC concentration data do not support the notion that reserves are also important in postfire sprouting, other circumstantial evidence suggests that belowground reserves do influence sprouting. First, even with considerable shading, biomass

production was nearly half that of those shrubs in full sunlight. Second, casual observation in July 1985 of a few of those shrubs whose entire aboveground biomass was harvested in October 1984 after one season of postfire growth, revealed that no sprouting had occurred in the second postfire year. Such a total lack of regrowth following both burning and harvesting suggests that either energy reserves or bud primordia can limit postfire sprouting. Repeated herbivory of chamise sprouts has produced similar results (Moreno and Oechel 1991). Perhaps current photosynthesis during the first postfire year accomplishes little toward replenishing those reserves that are utilized in sprouting, but instead simply augments postfire sprout production.

We have shown the potential for prefire shrub size and the proportion of standing dead biomass to influence postfire sprout production in *A. fasciculatum* shrubs. While our data do not demonstrate senescence in chamise shrubs, they provide evidence that stands having many sprouting shrubs with high proportions of standing dead biomass will tend to recover less vigorously after fire, perhaps due to a reduced ability in shrubs in these stands to sequester TNC reserves to support sprouting. Sparks et al. (1993) observed that shrubs in old stands of chaparral sequestered lower proportions of their leaf photosynthate into TNC during the spring, which could affect belowground accumulation of TNC reserves. Such old stands are, of course, likely targets of land managers using prescribed fire to reduce fuel hazards. While the amount of standing dead biomass alone is not a good predictor of chaparral stand age (Paysen and Cohen 1990), the proportion of shrubs having high components of standing dead biomass is nevertheless likely to increase with age for any particular stand; however, the rate at which the increase occurs may vary for different levels of site quality. Hence there may be some incentive to burn chaparral stands before high levels of standing dead biomass are reached, both to reduce fuel hazard and to promote vigorous postfire sprouting. Evidence of reduced sprouting capability in old individuals is also found for some hardwood tree species (Roth and Hepting 1943; Johnson 1977; Kays et al. 1988).

Obviously, other factors are probably also influential in postfire sprouting in the chaparral; our own data for chamise indicate the importance of current photosynthesis of sprouting shoots. Future research should focus on the effects of season and temperature of the prescribed fire. Our experimental burn was carried out under cool and wet conditions (actually a probable scenario for prescribed chaparral burns in general). A summer or fall burn could generate higher temperatures and perhaps increase sprouting shrub mortality to levels observed for chamise elsewhere (Keeley and Zedler 1978; Stohlgren et al. 1984; Moreno and Oechel 1991; only two chamise shrubs were killed in our burn). Finally, the interactions between

postfire sprouting vigor, nutrient availability, and fire temperature (which influences nutrient volatilization; DeBano et al. 1979; Dunn et al. 1979) need to be evaluated to maximize the efficacy of prescribed fire as a management technique in the California chaparral.

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HABITAT CHARACTERISTICS OF *EUTREMA PENLANDII* (BRASSICACEAE) IN THE COLORADO ROCKIES: A STUDY OF ALPINE ENDEMISM

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Abstract

The Mosquito Range of central Colorado contains a number of endemic and disjunct plant taxa. Among these is *Eutrema penlandii* (Brassicaceae), a species with arctic affinities known only from a few populations in the Mosquito Range. Previous studies predicted *Eutrema* was restricted to carbonate bedrock, but we found that an alkaline (carbonate) substrate is not a causative factor in the narrow endemism of this species. Critical environmental parameters include a continual supply of moisture from late snowbeds, and a cold microsite insulated by a bryophyte mat that retains moisture. These factors suggest that the species may be a Pleistocene relict with a currently limited amount of critical habitat. There is cause for concern about the future of this species in light of our climatic uncertainty.

Unusual bedrock often provides habitat for rare alpine plants. Ultramafic, carbonate, and highly mineralized soils in particular are known to be associated with endemic, often threatened or endangered, taxa. Although these habitat correlations are recognized, it is often difficult to determine whether the taxa require extraordinary edaphic conditions, or whether they are simply tolerant of them and thrive in low competition sites. The complex interaction of physiological, genetic, and environmental factors in plant endemism has been addressed by a number of authors (see, among others: De Silva 1934; Mason 1946; Bamberg and Major 1968; Kruckeberg 1954).

Endemism may also be the product of paleoecology as well as contemporary ecology. Hooker (1862), Fernald (1925), and Hultén (1937) were some of the first botanists to analyze arctic and alpine floristic relationships and to emphasize the role of Pleistocene environments in shaping modern plant distributions. Since these early papers, a number of other authors have discussed the arctic element in the alpine flora of North America (e.g., Dahl 1946; Weber 1965; Ives 1974; Löve and Löve 1974). However, origins and dispersal routes remain most easily analyzed on the basis of individual taxa. It is not yet, and may never be, possible to describe generalized paleoecological conditions that would explain the numerous cases of disjuncts, endemics, and arctic/alpine species pairs seen in our flora.

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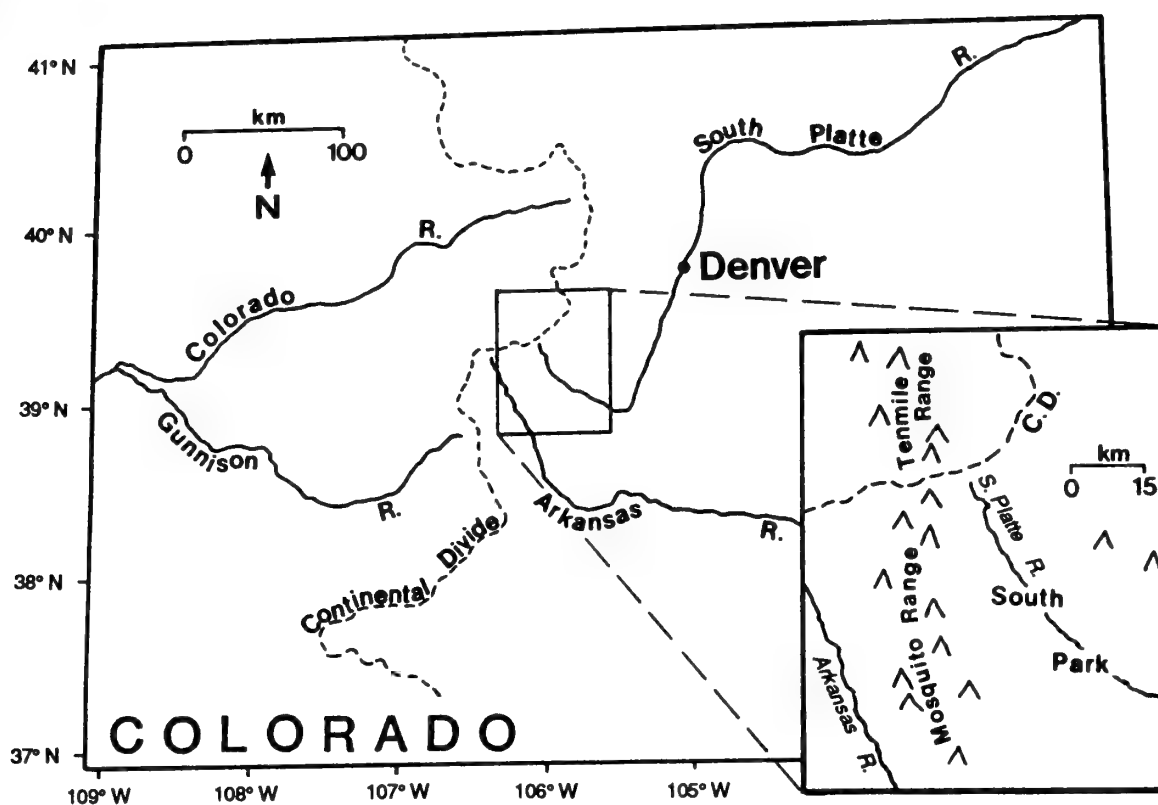
FIG. 1.   Location of Mosquito Range in Colorado.

The southern Rocky Mountains contain some unusual plant dis-
tributions which provide opportunities to assess the possible con-
tributions of edaphic and paleoecological factors in endemism. One
center of phytogeographical interest is the Mosquito Range of central
Colorado (Fig. 1). The range is noteworthy for its abundance of
endemic and disjunct arctic and boreal plant taxa (Thorn 1981;
Weber 1987, 1990). It also has an unusual abundance of carbonate
bedrock rare or absent elsewhere in the Colorado mountains. The
unusual flora there suggests an association with the bedrock, al-
though this relationship has not been demonstrated definitively for
any species.

Eutrema penlandii Rollins (Brassicaceae), also known as *E. ed-
wardsii* ssp. *penlandii* (R. Br.) Weber (Rollins 1950; Weber 1990) is
endemic to the Mosquito Range, with affinities to a circumpolar
arctic species complex. In North America, the closest relatives are
found 2000 km to the north in the Canadian Arctic Archipelago.

One phytogeographic scenario suggests that glacial advances pushed
cryophilous taxa like *Eutrema* and other taxa from the Arctic to the
Southern Rockies (Löve and Löve 1974). Whether this migration
was in the Pleistocene, or perhaps as early as the Tertiary (Weber
1987) is arguable. Within the Mosquito Range, valley glaciers were
common at different times (Capps 1909). Manley (1986) found mo-
raines to indicate ice cover 15,000–20,000 yr BP, and extensive
glacial evidence exists throughout the range. Many of the Pleistocene

moraines identified by Capps (1909) are adjacent to current populations of *E. penlandii.*

Given these conditions, it seems very unlikely that *Eutrema* could have existed in situ during the late Pleistocene. More probable habitat can be found at lower elevations in nearby South Park (Fig. 1). This high elevation (ca. 2900 m) grassland today supports other disjunct arctic and boreal species, including *Primula egaliksensis* Wormskj. and *Salix candida* Fluegge (Cooper 1991; Weber 1990). Radiocarbon dates from Lost Park bog in the nearby Tarryall Mountains indicate extensive vegetative cover there at least as early as 11,820 (±100) yr BP (Vierling and Sullivan 1992). If *Eutrema penlandii* is a Pleistocene relict, it may have migrated up in elevation with Holocene warming and glacial retreat.

Although *Eutrema penlandii* was first discovered in 1935, detailed studies of the species were not conducted until relatively recently when the Colorado Natural Areas Program initiated habitat and population surveys. The report by Naumann (1988) suggested federal listing as a threatened species because of the few known populations, low numbers of individuals in these populations, and the restricted habitat. A primary concern was an apparent correlation with carbonate bedrock and high elevation sub-irrigated soils. Acid mine drainage in the Mosquito Range then appeared to have the potential to alter the integrity of these alpine habitats.

Appropriate management of *Eutrema penlandii* required a precise determination of the habitat, in particular, its relationship to carbonate substrate. The study described here is our assessment of the habitat characteristics of this taxon. Our objective was to look for common environmental parameters in the known populations that might at least partially explain the distribution of *E. penlandii.* We specifically addressed the following:

1. Comparison of soil pH and moisture levels within and outside *Eutrema* populations.
2. Determination of associated bedrock.
3. Comparison of levels of exchangeable calcium within and outside *Eutrema* populations.
4. Description of local geochemistry through analysis of soil oxides and trace elements.
5. Determination of associated bryophyte taxa.

The close association of *Eutrema* and bryophytes was noted by Naumann (1988) as a consistent feature of the known populations; however, these bryophyte species were never collected or identified. Because at least some bryophytes are known to be good indicators of soil pH, we believed it critical to have identifications of all associated taxa.
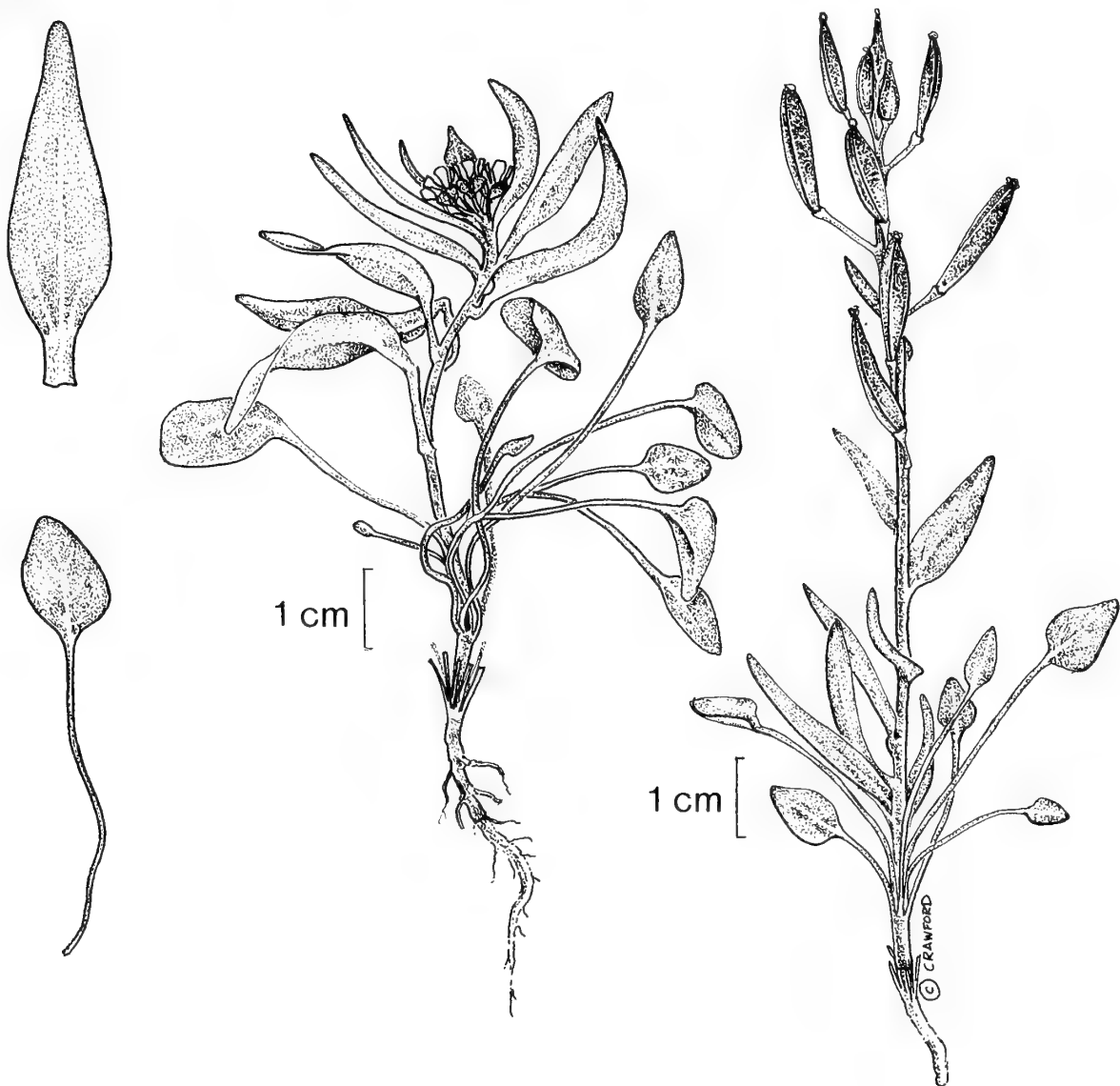
FIG. 2.   *Eutrema penlandii.*

STUDY SITES AND METHODS

Species description. Eutrema penlandii is an inconspicuous herbaceous perennial 2–10 cm high (Rollins 1950). It is distinguished from other white-flowered alpine members of the Brassicaceae by its glabrous nature, ovate, thinly petiolate basal leaves, sessile cauline leaves, and its elliptical quadrangular fruits (Fig. 2). Plants grow singly or in clumps of 2–5 individuals in a bryophyte or bryophyte-graminoid community. There is no evidence of vegetative reproduction. Populations contain from 50–2000 individuals and cover from 0.5 to ca. 16 ha in area (Naumann 1988).

Study sites. We used the eight previously documented populations of *Eutrema penlandii* (Naumann 1988) in the Mosquito Range between Hoosier Ridge and Mount Sherman for analysis. Within this area, *E. penlandii* is restricted to low angle east and south-facing

slopes between 3745 and 3939 meters. Deep snow accumulation on these leeward slopes provides persistent snowbeds lasting into July. Snowbed meltwater supports the bryophyte understory that is one of the few common elements among *Eutrema* populations.

Geological maps of the region (Tweto 1974; Tweto et al. 1978) indicate that *Eutrema penlandii* can be found on a number of geological formations, only some of which contain carbonates. These include the Minturn Formation (sandstone, shale, and scattered carbonates), the Belden Formation (shale, carbonates, and sandstone), Leadville Dolomite, the Maroon Formation (sandstone, mudstone, and conglomerate), and intrusive porphyries. The bedrock of the region is highly diverse; because most *Eutrema* populations occur below scree slopes, different formations can contribute to the underlying substrate.

Populations were studied in the field between 6 July 1991 and 30 July 1991 when flowers were in bloom; laboratory analyses were completed between July 1991 and January 1992.

In the field we measured slope and aspect, and flagged individual plants for population counts and determination of boundaries. Indicator mosses were collected in each population and sent to the University of Colorado Museum Herbarium (COLO) for identification. We collected 3 to 5 soil samples adjacent to *Eutrema* plants at a depth of 10 cm; samples were spaced equidistantly throughout the population. An equal number of control samples were taken 2–20 m outside each population. For sampling purposes, we treated subpopulations as distinct communities because they occurred several hundred meters apart. Location for peripheral samples was determined on the basis of the nearest floristically distinct plant community (defined as a change from bryophyte and bryophyte-graminoid community to a forb-dominated community). Due to the frequent occurrence near *Eutrema* populations of boulderfields, cliffs, standing water, and other sites inappropriate for comparative soil samples, we could not use a uniform sampling distance. Given the mosaic nature of these alpine habitats, we believe that subjective sampling using phytosociological criteria would provide the most useful comparison of botanically significant soil characteristics.

Analysis. In the laboratory, wet soil weight was measured immediately, and dry soil weight was measured after air drying for 48 hours when no further weight change was indicated. Soil moisture was calculated as: weight soil water/dry soil weight. After sieving out organic materials to ensure homogeneity, we mixed a 1:1 ratio of soil and distilled water, let the mixture settle for 20 minutes, then measured soil pH with an electronic pH meter. Exchangeable calcium was analyzed in a Varian 227B AA/AE Atomic Absorption Spectrometer following preparation procedures adapted from Moore and Chapman (1986).

To measure oxides and trace elements in the soil, samples were weighed, dried at 1100° overnight, and reweighed. They were then sieved to separate stones and undecomposed organic material, then ground to a powder. One g of powder was mixed with 9 g lithium tetraborate, fired at 1100° for 20 minutes to form a glass pellet, then analyzed using a Rigaku 3070 Spectrometer.

For statistical analysis, a log transformation of pH data was performed to compare mean pH with a two-tailed t-test (Sokol and Rohlf 1969). We also used two-tailed t-tests to measure the degree of difference between means of soil moisture and exchangeable calcium inside populations to the means in peripheral areas.

RESULTS

Twenty-two different bryophyte taxa representing 19 genera were identified in *Eutrema* populations. These were generally common alpine/subalpine taxa with no known affinity for unusual substrates, including *Mnium blyttii* B.S.G., *Didymodon asperifolius* (Mitt.) Crum, Steere and Anderson, *Aulacomnium palustre* (Hedw.) Schwaegr., *Entodon concinnus* (DeNot.) Paris, and *Bryum* spp. One species, *Brachythecium turgidum* is a calciphile (Vitt 1988), but was found only in populations at two locations.

The results of soil pH analyses are summarized in Table 1. Although t-tests on transformed data (Sokol and Rohlf 1969) show a slight statistical difference between samples within and around *Eutrema* populations ($P < 0.04$), the pH ranges are quite broad. Within populations, the pH of 48 samples ranged from 5.5 to 7.0, generally slightly acidic to neutral. Only 6 samples had a pH greater than 7, with a high of 7.9. Peripheral samples had a slightly broader range (4.6 to 8.0), from acid to alkaline.

Soil moisture levels are summarized in Table 1. Soils within populations ranged from 47% to 668% (with an outlier at 1660%), and peripheral samples ranged from 11% to 217%. Mean soil water content within populations was 338%, significantly higher than the mean of 75% found in peripheral samples (t-test, $P < 0.001$). However, the high variance of these soil moisture levels limit their usefulness for interpretation; the only significant result that we can conclude is that *Eutrema* is only found in sites that are consistently very wet; high moisture levels may be maintained at least in part by the associated bryophytes.

Exchangeable calcium varies a great deal within and around populations (Table 1). Samples within populations have a range of 1550–15,500 ppm, with a mean of 5800 ppm. Calcium in peripheral samples ranged from 155–10,850 ppm, with a mean of 3400. Although these means are statistically different (t-test, $P < 0.001$) the high variance and comparison with the potentially much greater levels of calcium in other known carbonate soils (Bowen 1966; Bam-

TABLE 1. HABITAT CHARACTERISTICS OF *EUTREMA PENLANDII*. P value represents 95% CI for t-test using log transformation of data.

	Within populations	Peripheral samples	P value
Soil pH			
Mean (SE)	6.33 (0.08)	6.05 (0.11)	<0.04*
Range	5.50–7.90	4.60–8.00	
n	48	41	
% Soil Moisture			
Mean (SE)	338.4 (52.1)	74.7 (11.0)	<0.000**
Range	47.0–1660.0	11.0–217.0	
n	31	29	
Exchangeable Calcium (ppm)			
Mean (SE)	5649 (443)	3365 (393)	<0.001**
Range	1178–15,500	155–10,850	
n	44	39	

Soil Composition
(n = 5; Samples taken from Pennsylvania Mt., Mosquito Pass, Mt. Sherman, Mt. Silverheels, and Hoosier Ridge *E. penlandii* populations)

Oxide	Mean % (SE)	Element	Mean ppm (SE)
NO_2	0.77 (0.34)	V	49.6 (10.7)
MgO	1.14 (0.15)	Cr	68.6 (27.7)
Al_2O_3	11.34 (0.73)	Co	8.8 (3.2)
SiO_2	45.20 (3.44)	Zn	133.6 (16.3)
P_2O_5	0.33 (0.05)	Rb	114.6 (8.9)
K_2O	2.55 (0.15)	Sr	181.0 (41.6)
CaO	1.92 (0.21)	Y	7.0 (2.3)
TiO_2	0.39 (0.06)	Zr	151.4 (13.5)
MnO	0.10 (0.02)	Nb	13.4 (1.3)
FeO_3	3.04 (0.57)	Ba	825.4 (226.0)

berg and Major 1968; Retzer 1974) suggest that *Eutrema* populations are not limited by the presence or absence of high levels of calcium.

The oxide and trace element composition of soils also appears to vary a great deal (Table 1). All levels are comparable to typical alpine soil profiles (Bowen 1966; N. Bower personal communication) and there is no indication of unusual geochemistry that would explain the endemism of *E. penlandii*.

DISCUSSION

Based on analyses of soil composition, pH, and available calcium, we cannot conclude there is any direct correlation between the occurrence of *Eutrema penlandii* and the presence of carbonate bedrock in the Mosquito Range. While we did find differences in soil pH and calcium levels between samples within and around *Eutrema*

populations, the range of values suggests that these parameters may not be biologically significant. Acidic to neutral pH values are typical for Colorado alpine soils (Johnson and Cline 1965). On carbonate parental material, pH sometimes reaches slightly alkaline levels but these may be buffered by organic acids in the peat in which *Eutrema* grows. The highly variable amounts of exchangeable calcium are low in comparison to other known carbonate soils (Bowen 1966).

Trace elements and oxide analyses give no indication of the presence of chemically anomalous substrate, and we can find no consistent correlation of the presence of *Eutrema* with any specific geological formation. While sometimes found on or near carbonate-rich bedrock (Manitou Dolomite, Belden and Minturn Formations), it is found equally often on other formations that do not contain carbonates.

Although this species is apparently *not* an obligate calciphile, there are other critical aspects of the habitat that may restrict its distribution. The consistently high moisture levels in *Eutrema* habitat suggest that continually wet soil may be one of the most important.

Low angle, high elevation leeward slopes are not common in the central Rockies; for example, both the adjacent Ten Mile and Collegiate Ranges have elevations comparable to those in the Mosquito Range, but the former generally contain steep, unstable lee slopes where snow does not accumulate deeply. In addition, these ranges are oriented more north-south than the Mosquito Range, which has a northeast-southwest trend. As Weber (1987) noted, this orientation results in slower snow melt and more available moisture in the growing season, as well as winter protection from desiccating chinook winds.

Accumulation of deep snowfields is a critical aspect of *Eutrema* habitat: these snowfields provide a constant source of moisture that nourishes bryophyte communities. The mat of bryophytes in turn holds moisture and provides a cold, continually wet microsite necessary for *Eutrema* populations. *Eutrema* also appears to prefer sites with low competition from other forbs. This combination of factors is uncommon even in the Mosquito Range. As a result, the rarity of *Eutrema* populations may be due to the limited amount of appropriate microhabitat even though there are broad expanses of south and east-facing slopes.

CONCLUSIONS

Whatever its origin, *Eutrema penlandii* is a striking reminder of the complex affinities of the Colorado flora. We find no evidence from this comparative study of the few known populations of *Eutrema penlandii* that it is restricted in its distribution by dependence on alkaline bedrock or unusual geochemistry. This should encourage

botanists to continue to look for it elsewhere in the central Rockies. However, based on what we have observed, the species does appear to be dependent on the availability of wet, low angle, low competition, high elevation sites. An intensive search for additional populations of *E. penlandii* in the summer of 1991 by numerous personnel from the Alma American Mining Company and the Colorado Native Plant Society neither revealed significant new populations in the Mosquito Range or surrounding mountains, nor led us to reassess the low population numbers given in the original status report.

We find the few populations, low numbers of individuals, and apparent sensitivity to moisture availability in this species reason for concern, especially as our global climatic uncertainties may add further stress to plant taxa already restricted to sensitive microhabitats. As Schoonmaker and Foster (1991) suggest, paleoecological histories can have considerable relevance for understanding contemporary ecological changes. While *Eutrema penlandii* is only one of the many species in the Mosquito Range with individual histories and individual ecologies, we suggest that it is an important one that deserves habitat protection. This species, and the Mosquito Range flora as a whole, warrant future attention from ecologists and phytogeographers.

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HOLOCENE CHANGES IN THE FLORA OF RAGGED TOP, SOUTH-CENTRAL ARIZONA

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Abstract

A total of 73 plant taxa were identified from three packrat (*Neotoma* sp.) middens radiocarbon dated between 14,550 and 5020 yr B.P. from Wolcott Peak in Ragged Top, Pima County, Arizona. Most (80.1%) of the plants still grow in the area although only 17.8% still occur at the midden site. Fourteen late Wisconsin woodland/chaparral species (19.2%) were locally extirpated in the Holocene. Today five (6.5%) occur in nearby (<5 km), five in moderately distant (<40 km), and four (5.5%) in more distant (90–135 km) mountain ranges. *Agave deserti* was associated with *Juniperus osteosperma, Opuntia whipplei,* and *Pinus monophylla* in the late Wisconsin but their ranges no longer overlap. The Ragged Top flora shifted composition in the Holocene as woodland species died out and Sonoran desertscrub species arrived at different times. Relict populations of *Quercus turbinella, Vauquelinia californica,* and *Yucca baccata* reflect cooler, winter-rainfall ice age climates prior to about 8900 years ago. Isolated populations of *Echinopepon wrightii, Ipomoea cristulata,* and *Pisonia capitata* were likely established by chance seed dispersals 4000 to 8900 years ago in more subtropical climates of the middle Holocene.

Seeds, fruits, leaves, twigs, and spines preserved in ancient packrat (*Neotoma* sp.) middens have provided a rich fossil record for plants that grow on rocky slopes in the North American deserts for the last 40,000 years (Van Devender et al. 1987). In the Sonoran Desert, woodlands dominated by *Pinus monophylla* (singleleaf pinyon), several species of *Juniperus* (junipers), and *Quercus turbinella* (shrub live oak) descended to 600 m elevation, about 600 m lower than modern woodlands, during the Wisconsin glacial period (>43,000 to about 11,000 years ago; Van Devender 1990). A xeric woodland with *J. californica* (California juniper), *Yucca brevifolia* (Joshua tree), and *Larrea divaricata* Cav. (creosotebush) occurred down to about 300 m. Desertscrub dominated by *L. divaricata* and *Ambrosia dumosa* (white bursage) were likely to have been present in lower areas along the Colorado River throughout the Pleistocene (Cole 1986; Van Devender et al. 1990).

After about 8900 years ago in the middle Holocene, desertscrub communities developed in the northeastern Sonoran Desert in Arizona. The last woodland/chaparral plants moved upslope as important Sonoran species including *Carnegiea gigantea* (saguaro), *Cercidium floridum* (blue paloverde), and *Encelia farinosa* (brittlebush) returned from their ice age refugia, presumably in Sonora,

Mexico. Relatively modern Sonoran desertscrub communities did not form until about 4000 years ago in the late Holocene with the arrival of *C. microphyllum* (foothills paloverde), *Stenocereus thurberi* (organpipe cactus), and other more subtropical desert species.

In the northeastern Sonoran Desert in Arizona, the landscape is a mosaic of mountain ranges adjacent to broad valleys, or emergent from desert plains. Mountain slopes typically support rich mixed desertscrub dominated by *Carnegiea gigantea* and *Cercidium microphyllum* while sparse lowland communities are dominated by *Larrea divaricata* (Shreve 1964; Turner and Brown 1982). Species that live in rocky habitats often have discontinuous distributions restricted to the mountains. Some of the isolated populations are plants typically found in woodland, chaparral, or more subtropical desertscrub (Brown 1978) that may reflect favorable climates in the past or chance dispersals. Our survey of the flora of Ragged Top, a rugged desert peak in the northeastern Sonoran Desert, yielded a number of interesting isolated plants (Wiens 1990). In an attempt to understand the developmental history of the Ragged Top flora and to provide insight into the timing of isolation of the relicts, we examined the plant macrofossils in packrat middens from Wolcott Peak, a secondary peak in Ragged Top. Here we present the results of those analyses and discuss their biogeographical implications.

Study Area

Geology. Ragged Top is a steep, rugged desert mountain in Pima County, Arizona, approximately 6.5 km north of Silver Bell and 50 km northwest of Tucson (Fig. 1). It is bordered on the east and north by Avra Valley and on the west and south by the Silver Bell Mountains, a desert range, composed of Cretaceous volcanics and granodiorite, reaching 1300 m elevation. Ragged Top rises to 1190 m while Wolcott Peak on the southeast side reaches 1015 m (Fig. 2). The north and east slopes of Ragged Top are middle Precambrian granite, while the south and west bajadas are mainly Quaternary alluvium and talus. The range itself is composed of a deeply weathered ridge of Tertiary intrusive rhyolite which is mostly oriented east to west (Nowlan et al. 1989). North–south fractures and subsequent weathering have formed many small clefts and deep canyons. Packrat middens were found preserved in the dry crevices and rockshelters.

Climate. The climate of Ragged Top is characteristic of the northeastern Sonoran Desert, with infrequent winter freezes, hot summers, and biseasonal rainfall (Sellers and Hill 1974; NOAA 1980). During summer, equatorial heating strengthens the subtropical Bermuda High moving moist air masses both westward from the Gulf of Mexico across the continent and north-northeastward from the Gulf of California in a pronounced summer monsoon. In winter,
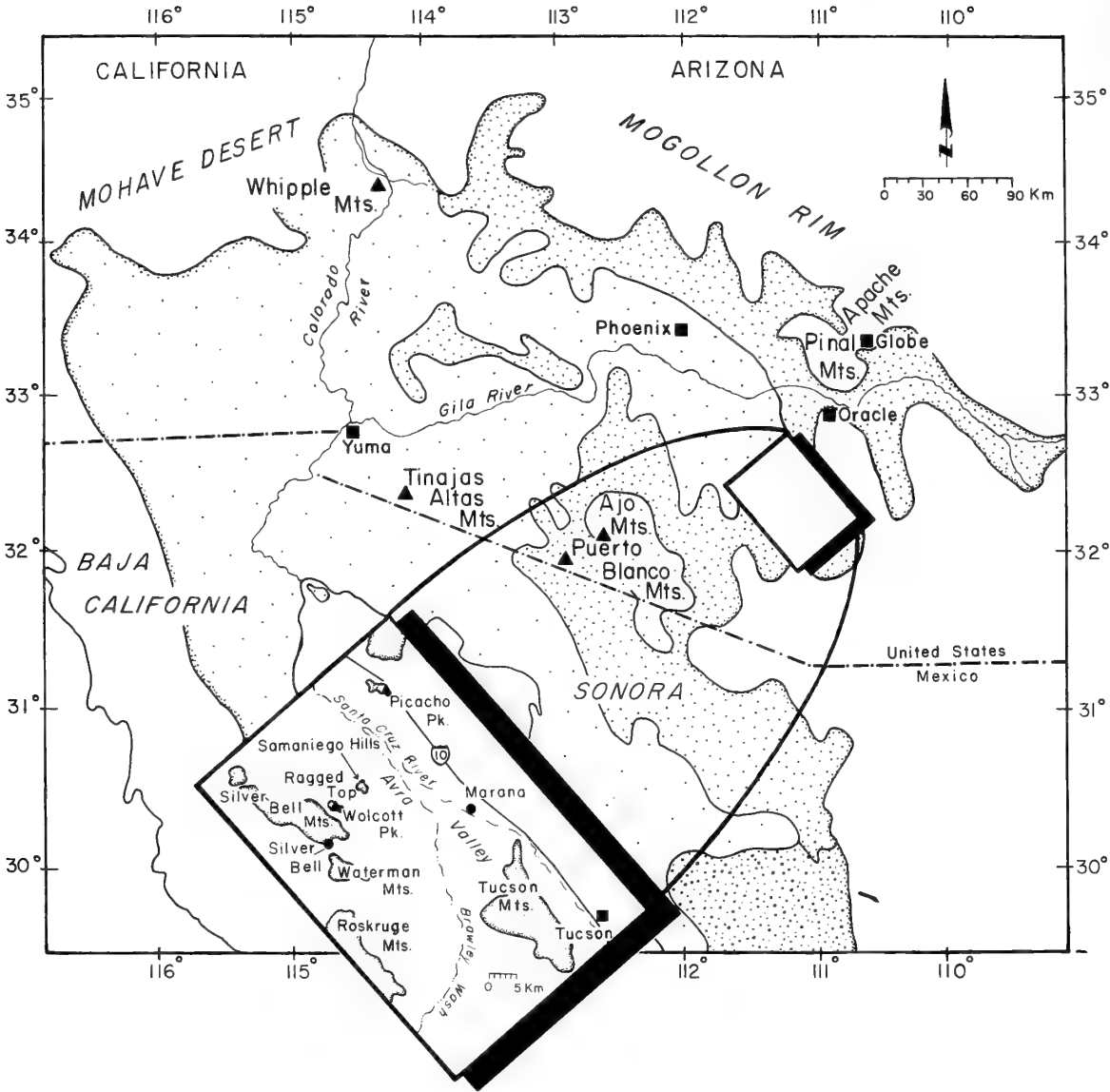
Fig. 1. Map of the study area. Arizona Upland subdivision of Sonoran Desert in heavy stipple; Lower Colorado River Valley in light stipple.

precipitation arrives from frontal storms moving east from the Pacific Ocean. The mean annual precipitation for Silver Bell at 825 m elevation is 312 mm/yr with 51.3% falling from July through September. Mean temperatures are 27.4°C annual, 17.3°C for January, and 37.3°C for July.

Vegetation. Ragged Top is in the Arizona Upland subdivision of the northeastern Sonoran Desert (Shreve 1964; Turner and Brown 1982). The desertscrub on the lower bajada is dominated by *Cercidium microphyllum*, *Ambrosia deltoidea* (triangleleaf bursage), and *Carnegiea gigantea* in association with *Cercidium floridum, Olneya tesota* (ironwood), and *Prosopis velutina* (velvet mesquite) along major washes. On steep, south-facing slopes *Encelia farinosa* (brittlebush) is also important. *Acacia greggii* (catclaw acacia), *Celtis pallida* (desert hackberry), and *Lycium berlandieri* (wolfberry) are common

A.

B.

FIG. 2.   A. View of the southern slopes of Ragged Top and Wolcott Peak from the Silver Bell Mountains. B. View of study area from southeast. Typical Arizona Upland desertscrub in foreground with *Carnegiea gigantea, Cercidium microphyllum,* and *Fouquieria splendens.*

at cliff bases near the midden sites in association with *Acacia con-stricta* (whitethorn acacia), *Ambrosia ambrosioides* (canyon rag-weed), *Fouquieria splendens* (ocotillo), *Horsfordia newberryi* (yellow felt plant), *Hyptis emoryi* (desert lavender), *Larrea divaricata, Sim-mondsia chinensis* (jojoba). Succulents include *Carnegiea gigantea, Ferocactus wislizeni* (fishhook barrel), and a variety of *Opuntia* spp. (chollas and prickly pears).

The north-facing slopes and canyons of Ragged Top provide mesic microhabitats. Shady, cool vertical cliffs, often more than 30 m tall, shelter *Brickellia californica* (brickell bush), *Celtis pallida, Eriogo-num fasciculatum* (California buckwheat), *Forestiera shrevei* (desert olive), *Opuntia chlorotica* (pancake prickly pear), *Prosopis velutina, Quercus turbinella, Vauquelinia californica* (Arizona rosewood), *Yucca baccata* var. *brevifolia* (Schott) Benson & Darrow (banana yucca). Most of these are relict species more typical of desert grass-land and chaparral communities at higher elevations.

In Avra Valley at the lower end of the bajada, the vegetation changes to a xeric desertscrub characteristic of the Lower Colorado River Valley subdivision. Dominants include *Larrea divaricata, Ambrosia dumosa, Olneya tesota, Hymenoclea salsola* (cheesebush), and, in grazed areas, *Isocoma tenuisecta* (burroweed).

Packrat middens. Packrats or woodrats are medium-sized rodents in the genus *Neotoma* (Cricetidae) that collect various plant materials for food and construction of a house or den (Finley 1958). When packrats live in dry rockshelters, urination perches in the dens can become indurated by urine into hard, dark, organic deposits termed middens. Plant remains in such middens provide excellent samples of the local vegetation within about 30 m of the rockshelter filtered through a packrat's dietary preferences and collecting habits.

When middens are carefully collected from discrete stratigraphic units and outer surfaces are removed, contamination is not a serious problem. Improvements in sampling and radiocarbon dating meth-ods in the last 20 years have reduced contamination to a minimum. Radiocarbon dates on very small samples using the tandem accel-erator mass spectrometer permit the antiquity of or contamination by individual species to be verified (Van Devender et al. 1985).

METHODS

The Wolcott Peak samples were collected in 1971 before standard procedures to prevent contamination were developed (Van Deven-der 1973). Samples were collected from crevices at 860 m elevation facing south (WP2) and southwest (WP4, WP5). In the WP2 sample, several small chunks of midden from a deep narrow cleft were com-bined because of their similar appearance and unusual abundance of bone (Van Devender and Mead 1978; Mead et al. 1983). Midden

debris from the WP2 yielded an age of 5020 ± 80 yr B.P. (A–1216, radiocarbon years before 1950), several thousand years younger than expected for a juniper assemblage from a desert site. A separate date of 14,550 ± 800 yr B.P. (A–1286) on juniper twigs confirmed mixing of material of different ages. Radiocarbon dates on the other samples were: WP4: 5350 ± 100 yr B.P. (A–1236 on midden debris) and WP5: 12,130 ± 500 yr B.P. (A–1287 on *Juniperus* twigs).

Midden samples were disaggregated in water, washed through a 20 mesh soil sieve, air dried, and sorted under a binocular microscope. Plant specimens were identified using reference specimens in the Herbarium and the Desert Laboratory at the University of Arizona. Distributions for extralocal species were determined using specimens in the Herbarium and the literature. Plant fragments were ranked in an internal relative abundance scale ranging from rare to abundant: i.e., a single specimen ranked 1, the most common taxon 5, the remainder in between. More elaborate quantitative methods using percentages of identified specimens greatly increase the analytical effort without significantly improving the final result (Spaulding et al. 1990; Van Devender 1990).

The modern flora above 720 m elevation was surveyed briefly in 1971 and intensively from 1987 through 1992. Vouchers of modern plant specimens were deposited into the herbaria at the Arizona–Sonora Desert Museum and the University of Arizona. Species encountered near the midden sites are presented in Table 1. Plant nomenclature follows Lehr (1978) with authorities for exceptions given in the text or tables.

Results and Discussion

The plant macrofossils from the packrat middens provide glimpses of the flora and vegetation of Wolcott Peak at two times in the past, and help understand the history and development of a complex flora. A total of 73 plant taxa, including trees and woody shrubs (19.2%), subshrubs (9.6%), succulents (13.7%), herbs (41.2%), and grasses (16.4%) were identified from the three midden assemblages (Table 1). The number of taxa identified per midden ranged from 11 to 54 (av. = 35.7).

Late Wisconsin. The mixed WP2 assemblage yielded several typical woodland plants including *Berberis* sp. (barberry), *Juniperus erythrocarpa* Cory/*J. monosperma* (redberry/oneseed juniper), *J. osteosperma* (Utah juniper), and *Pinus monophylla*. Considering that these species are typical of late Wisconsin midden assemblages in the northeastern Sonoran Desert (Van Devender 1990; Anderson and Van Devender 1991; Van Devender et al. 1991), they were probably associated with the 14,550 yr B.P. date rather than the 5020 yr B.P. middle Holocene date.

TABLE 1. PLANTS IDENTIFIED FROM THE SITE AND IN PACKRAT MIDDENS FROM WOLCOTT PEAK, PIMA COUNTY, ARIZONA. Relative abundances: 1 = rare, 2 = uncommon, 3 = common, 4 = very common, 5 = abundant. Distribution codes: n = present at the midden site, WP = elsewhere on Wolcott Peak and surrounding bajada, RT = not on Wolcott Peak, but elsewhere on Ragged Top, SH = Samaniego Hills (4.5 km NE), SB = Silver Bell Mountains (3.5 km S), WM = Waterman Mountains (10 km S), TM = Tucson Mountains (35 km SE), e = extralocal, no longer in the nearby ranges. * = species in a midden sample; ka = thousands of years (radiocarbon dates in text).

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6 ka)	WP2 (5.0 ka)	WP4 (5.3 ka)
Trees and shrubs							
*Acacia greggii	Catclaw acacia	Leaflets, thorns	3		2WP		
*Berberis sp.	Barberry	Seeds, leaflets			2e		
*Celtis pallida	Desert hackberry	Seeds, fruits, leaves	2	3n	3n		2WP
Cercidium microphyllum	Foothills paloverde		3	2RT			
*Condalia warnockii	Mexican crucillo	Seeds	2				
Crossosoma bigelovii	Rhyolite bush			2n	2n		1n
*Encelia farinosa	Brittlebush	Achenes	5				
*Eriogonum fasciculatum	California buckwheat	Leaf		1WP			
Horsfordia newberryi	Yellow felt plant		2				
Hyptis emoryi	Desert lavender		2				
*Juniperus erythrocarpa Cory/ monosperma	Redberry/oneseed juniper	Seeds, twigs		5e	5e	3e	3e
*Juniperus cf. osteosperma	Utah juniper	Seeds, twigs	3				
Larrea divaricata Cav.	Creosotebush		3				
Lycium berlandieri	Wolfberry						
*Lycium sp.	Wolfberry	Seed, twig	2	2n			
Olneya tesota	Ironwood						
*Pinus monophylla	Singleleaf pinyon	Nuts, needles		2e	2e		
*Prosopis velutina	Velvet mesquite	Mesocarps, leaflets		1WP	2WP		

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
*Quercus turbinella	Shrub live oak	Acorns, leaves, twigs		3WP	2WP	3
*Rhus cf. aromatica Ait.	Skunkbush	Seeds		2TM		
Simmondsia chinensis	Jojoba		4			
*Vauquelinia californica	Arizona rosewood	Fruits, leaves		3RT		
			n = 11	11	9	3
Subshrubs and woody vines						
Bebbia juncea	Sweetbush		1			
*Abutilon incanum/malacum Wats.	Indian mallow	Seeds, carpels	2	2WP	2WP	
*Brickellia cf. coulteri	Brickell bush	Involucres, twig	2	1n	2n	
*Carlowrightia arizonica		Capsule			1WP	
Cynanchum arizonicum (Gray) Shinners	Milkweed vine		1			
Ditaxis lanceolata (Benth.) Pax & Hoffman	Lanceleaf ditaxis		2			
*Ericameria cuneata	Cuneate turpentine bush	Involucres, leaves, twigs		4n	1WP	1WP
*Ericameria laricifolia	Turpentine bush	Leaf, twig	3	2n	1WP	
Eriogonum wrightii	Wild buckwheat		3			
Eupatorium solidaginifolium	Boneset		1			
Galactia wrightii			1			
Galium stellatum	Desert bedstraw		3			
Gymnosperma glutinosum	Tatalencho		2			

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
*Janusia gracilis	Desert vine	Fruits			2WP	
*Plumbago scandens	Leadwort, hierba de alacran	Fruit			1WP	
Stephanomeria pauciflora	Desert straw		1			
Trixis californica			3			1
			n = 12	4	6	1
Succulents						
*Agave cf. deserti	Desert agave	Leaves, hooks		3WM	1WM	
*Carnegiea gigantea	Saguaro	Seeds	2	2n	2n	5n
Echinocereus nicholii	Golden hedgehog		3			
*Ferocactus cylindraceus (Engelm.) Orcutt	California barrel cactus	Seeds		2SH		
*Ferocactus wislizeni	Fishhook barrel cactus	Seed	1	1WP		
*Mammillaria grahamii	Fishhook pincushion	Seeds	1		2WP	
*Opuntia acanthocarpa	Buckhorn cholla	Seeds	2	2WP	2WP	
*Opuntia bigelovii	Teddy bear cholla	Seed	3		1n	
*Opuntia chlorotica	Pancake prickly pear	Seeds	1	4WP	3WP	2WP
*Opuntia phaeacantha	Variable prickly pear	Seeds		2WP	5WP	2WP
Opuntia cf. spinosior × versicolor	Hybrid cholla		1			
*Opuntia cf. whipplei	Whipple cholla	Seeds		1e	2e	
			n = 8	8	8	3
Grasses						
Aristida adscensionis	Six-weeks threeawn		3			

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
Aristida parishii/purpurea	Threeawn	Floret	2			
*Bouteloua barbata	Six-weeks grama	Floret			1WP	
*Bouteloua curtipendula	Sideoats grama	Florets			1WP	1WP
*Bouteloua cf. repens	Slender grama	Florets			2RT	
*Brachiaria arizonica (Scribn. & Merr.) S. T. Blake	Arizona panicgrass	Florets		2WP	2WP	
*Bromus carinatus	Arizona brome	Florets		2WP		
Bromus rubens	Red brome		3			
*Digitaria cognata (Schult.) Pilg.	Fall witchgrass	Florets		2WP		
*Eriochloa acuminata (Presl.) Kunth.	Cupgrass	Floret			1SB	
*Hordium pusillum	Little barley	Florets		2TM		
*Panicum hirticaule	Witchgrass	Florets		2WP	2WP	
Poa bigelovii	Bigelow bluegrass		3			
Schismus barbatus	Mediterranean grass		3			
*Setaria leucopila	Bristlegrass	Florets	3	4n	4n	2WP
*Stipa speciosa	Desert needlegrass	Floret		1RT		
Vulpia octoflora	Six-weeks fescue		3			
*Vulpia sp.	Fescue	Floret		1WP		
			n = 7	8	7	2
Herbaceous perennials						
*Ambrosia confertiflora	Slimleaf bursage	Burs		2RT		
*Anemone tuberosa	Windflower	Seeds		2WP		
*Artemisia ludoviciana	White sage	Leaves		2SB		
Ayenia filiformis			2			

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/ 5.0 ka)	WP4 (5.3 ka)
*Cirsium sp.	Thistle	Achenes, phyllaries		2TM		
*Datura wrightii Regel	Sacred datura	Seeds		3TM		
Herissantia crispa	Wishbone bush		2			
Mirabilis bigelovii			3			
*Nicotiana trigonophylla	Desert tobacco	Fruits	2		2n	
Notholaena standleyi	Standley cloak fern		2			
Penstemon parryi	Parry penstemon		3			
Siphonoglossa longiflora			1			
*Solanum elaeagnifolium	Horse nettle	Seed		1SB		
*Tragia sp.	Noseburn	Seeds		2WP		
			n = 7	7	1	0
Perennial/annual herbs						
*Allionia incarnata	Trailing four o'clock, windmills	Seeds			2RT	
*Castilleja/Orthocarpus	Indian paint brush/owl clover	Seeds		2WM		
Ditaxis neomexicana (Muell.-Arg.) Heller		Seeds	1			
Eriogonum abertianum			3			
*Eriogonum inflatum	Desert trumpet	Fruit	3		1WP	
Euphorbia arizonica	Spurge	Seeds, fruits		2RT	2RT	
*Euphorbia melanadenia	Spurge					
Phaseolus filiformis	Bean		2			
*Physalis sp.	Ground cherry	Seeds		2WP	2WP	

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/5.0 ka)	WP4 (5.3 ka)
*Sphaeralcea sp.	Globe mallow	Carpels	3	2WP	2WP	
Verbena gooddingii	Vervain					
*Verbena sp.		Nutlet			1WP	1WP
			n = 5	4	6	0
Annuals						
*Amsinckia tessellata	Fiddleneck	Nutlets	2	2WP	2WP	1WP
Antirrhinum nuttalianum	Snapdragon		2			
*Boerhavia erecta L. var. intermedia (Jones) K. & P.	Spiderling	Fruits		2WP	2WP	
*Boerhavia wrightii	Spiderling	Fruit			1RT	
*Bowlesia incana	Hairy bowlesia	Seeds	2			2WP
Camissonia californica						
Camissonia chamaenerioides	Long-capsule primrose		3			
Caulanthus lasiophyllus (H. & A.) Payson			3			
Chenopodium neomexicanum	Fishy goosefoot		4			
*Cryptantha barbigera	Bearded nievitas	Nutlets	2	2WP		
*Daucus pusillus	Wild carrot	Mericarps	2	2WP	2WP	
Descurainia pinnata	Tansy mustard		1			
Draba cuneifolia	Whitlow grass		2			
Erodium cicutarium	Filaree					
*Erodium texanum	Stork's bill	Seed	4	1WP		
Eucrypta chrysanthemifolium	Torrey eucrypta		3			
Eucrypta micrantha	Smallflower eucrypta					
*Euphorbia revoluta	Spurge	Seed	2	1WM		
Filago californica						

Table 1. Continued.

Species	Common Name	Material	Site	WP5 (12.1 ka)	WP2 (14.6/5.0 ka)	WP4 (5.3 ka)
*Galium aparine	Bedstraw	Seed	2	1WP		
Gilia stellata						
*Kallstroemia sp.	Summer poppy	Seeds, leaves	2	4WP	2WP	
*Lupinus sp.	Lupine	Seeds		2WP		
Malacothrix clevelandii			2			
Oenothera primiveris	Large yellow desert primrose		1			
Parietaria hespera	Pellitory		2			
Perityle emoryi	Rock daisy		1			
Phacelia crenulata	Caterpillar weed		3			
Phacelia distans	Caterpillar weed		2			2n
*Phacelia sp.	Caterpillar weed	Seeds	2			
Pholistoma auritum						
*Plagiobothrys arizonicus	Bloodweed	Nutlet		1RT		
*Plantago fastigiata Morris	Indian wheat	Seeds		2WP		
Senecio lemmoni	Grounsel		2			
Silene antirrhina	Sleepy catchfly		3			
Spermolepis echinata	Scaleseed		2			
Steptanthus carinatus	Silver bells		2			
Stylocline micropoides	Desert nest straw		3			
*Thysanocarpus curvipes	Lacepod	Fruit	3	1WP		
Vicia ludoviciana	Vetch		2			
			n = 28	12	5	2
			Total = 78	54	42	11

The 12,130 yr B.P. sample yielded remains typical of a late Wisconsin pinyon–juniper–oak woodland/chaparral dominated by *Juniperus erythrocarpa/J. monosperma, Ericameria cuneata* (cuneate turpentine bush), and *Opuntia chlorotica,* in association with *Pinus monophylla, Quercus turbinella, Rhus* cf. *aromatica* Ait. (skunkbush), *Vauquelinia californica,* and *Agave* cf. *deserti* (desert agave). Leaves originally reported as *Q.* cf. *emoryi* (Emory oak) and *Rhamnus crocea* (hollyleaf buckthorn) in Van Devender (1973) were reexamined and found to be within the range of variation of *Q. turbinella.* Considering the Holocene radiocarbon ages associated with *Carnegiea gigantea* and *Encelia farinosa* in other northeastern Sonoran Desert midden studies (Van Devender et al. 1985; Van Devender 1990; Anderson and Van Devender 1991), the few seeds and achenes in WP5 probably represent younger contaminants and not members of the late Wisconsin flora. However, leaflets and seeds of *Prosopis velutina,* a desert grassland dominant, may be contemporaneous considering a radiocarbon date of 11,740 yr B.P. on *P. velutina* mesocarps from a Waterman Mountains midden (Anderson and Van Devender 1991).

The rugged topography and varied microhabitats of Ragged Top have greater potential for the survival of relict populations than nearby larger ranges. Only 24.1% of the 54 taxa in the WP5 sample no longer occur on the mountain. Of the WP5 taxa that still occur on Ragged Top, 53.7% still grow on hot south-facing slopes, including four of five local succulents. Today the south slopes of Wolcott Peak are too hot and dry to support 19 species (46.3%) now restricted to cooler more mesic microhabitats on north slopes and in riparian drainages. The relict plants include shrubs (*Eriogonum fasciculatum, Quercus turbinella, Vauquelinia californica*), a succulent (*Opuntia chlorotica*), grasses (*Bromus carinatus, Stipa speciosa*), perennial herbs (*Ambrosia confertiflora, Physalis crassifolia, Tragia nepetaefolia*), and annuals (*Boerhavia wrightii, Galium aparine, Kallstoemia* spp., and *Plagiobothrys arizonicus*). The relict *Q. turbinella* population contains eight mature plants. *Stipa speciosa* (desert needlegrass) is restricted to a few rocky outcrops on the north side. *Digitaria cognata* (Schult.) Pilg. (fall witchgrass) was only found in a wash on Wolcott Peak.

Overall, the responses of the plants in the Ragged Top flora to Holocene climate changes were modest. The plants that no longer live on Ragged Top represented only 19.2% of the midden flora, but included important structural components in late Wisconsin communities; i.e., trees, shrubs, and large succulents. The distances and directions to their nearest modern populations are of special biogeographical interest. Five species (6.5%) are found on nearby ranges within five kilometers. Another five species can be found on ranges within 40 kilometers. Only four species (5.5%) occur further away (90–135 km).

The absences of the succulents *Agave deserti* and *Ferocactus cylindraceus* (Engelm.) Orcutt (California barrel cactus) on Ragged Top are not easily explained. *Ferocactus cylindraceus* is found as low as 700 m elevation on most of the nearby desert peaks and hills including the Samaniego Hills (4.5 km NE). *Agave deserti* is still found in the Waterman Mountains in a variety of habitats from north-facing granitic slopes to south-facing xeric limestone. The absence of the widespread *Artemisia ludoviciana* (white sage, estafiate) is surprising considering its leaves in the WP5 sample, suitable shady niches on Ragged Top, and extensive populations on the north-facing slopes on the upper elevations of the Silver Bell Mountains (3.5 km S).

The remaining extralocal taxa all occur within 140 km. *Opuntia whipplei* (Whipple cholla) is reported from near Oracle (90 km ENE) but is more typically found in the northern half of Arizona (Benson 1982). A single *Juniperus erythrocarpa* (as *J. monosperma*) reported in the Silver Bell Mountains (3.5 km S; Brown 1978) has not been relocated. Otherwise, the nearest *J. erythrocarpa* occurs as relict populations on Newman Peak in the Picacho Mountains (35 km NNE; Brown 1978). *Pinus monophylla* can be found as close as the Pinal Mountains near Miami (110 km NNE) and on Table Mountain above Aravaipa Canyon (110 km ENE). The most distant of all the identified extralocal species is probably *J. osteosperma,* found as close as the Apache Mountains near Globe (135 km NNE; Little 1971). A specimen from between Vail and Saguaro National Monument (80 km ESE) in the University of Arizona Herbarium was annotated to *J. osteosperma* by Robert P. Adams in 1975. We feel that the identification or the locality is incorrect because *J. erythrocarpa* was the only species reported in the area by Bowers and McLaughlin (1987) in their extensive flora of the nearby Rincon Mountains.

Associations of two or more plants in late Wisconsin woodlands that cannot be found today or are limited to small ecotonal areas today have been reported in several Arizona Upland midden studies, including the nearby Waterman Mountains (Van Devender 1990). Contamination in the Wolcott Peak middens limited inferences of paleoassociations to obvious extralocal woodland/chaparral and winter-rainfall desertscrub taxa. In these assemblages the apparent associations of *Agave deserti* with *Juniperus osteosperma, Opuntia whipplei,* and *Pinus monophylla* appear to be anomalous. The ranges of *A. deserti, J. erythrocarpa,* and *Vauquelinia californica* only overlap in the upper portions of the Ajo Mountains in Organ Pipe Cactus National Monument (110 km WSW; Bowers 1980).

The percentage of trees and woody shrubs (20.4%) in WP5 is nearly twice that of Wolcott Peak (10.6%) and Ragged Top (11.2%) today while herbaceous perennials have been relatively constant (ca. 13%)

over time. However, the low semi-woody plants, here termed sub-shrubs, increased over two-fold although combined perennial non-succulents remained relatively constant: late Wisconsin = 40.7%, middle Holocene = 36.4%, Wolcott Peak flora = 41.8%, Ragged Top flora 39.4%. Percentages of woody perennials similar to those in the late Wisconsin Wolcott Peak woodland assemblages were found in four Waterman Mountains samples dated at 11,510 to 12,690 yr B.P. (44.7%; Anderson and Van Devender, 1991) and in two Picacho Peak (25 km NNE) samples dated at 11,100 to 13,170 yr B.P. (38.7%; Van Devender et al. 1991). In contrast, grasses and succulents were better represented in the Ragged Top flora in the late Wisconsin than today.

Middle Holocene. The WP4 sample yielded remains of a Sonoran desertscrub at a rocky cliff base at 5350 yr B.P. The plant assemblage was depauperate because of small sample size and the unusual abun-dance of bones (Van Devender and Mead 1978; Mead et al. 1983). Twigs of *Juniperus erythrocarpa/monosperma* in the sample were probably contaminants older than 8900 yr B.P. (Van Devender 1990) although rugged topography may have allowed a relict population to survive on Ragged Top later in the Holocene than in other ranges. Several plants sampled including *Celtis pallida, Ericameria larici-folia* (turpentine bush), *Opuntia chlorotica,* and *O. phaeacantha* (variable prickly pear) still occur on Wolcott Peak but not at the midden site, indicating more favorable moisture conditions than today.

A number of desertscrub or subtropical species that are fairly intolerant of freezes and cool, dry summers in the mixed WP2 as-semblage were likely associated with the 5020 yr B.P. date rather than the late Wisconsin 14,550 yr B.P. date. They include shrubs (*Celtis pallida, Prosopis velutina*), subshrubs (*Brickellia* cf. *coulteri, Carlowrightia arizonica, Plumbago scandens*), a perennial vine (*Ja-nusia gracilis*), and herbs (*Allionia incarnata, Boerhavia erecta* var. *intermedia, Nicotiana trigonophylla*). *Allionia incarnata, Janusia gracilis,* and *Prosopis velutina* are present elsewhere on Wolcott Peak or Ragged Top but no longer occur near the midden site. *Celtis pallida* appears to have been more common in the past than it is today. Indicators of greater moisture in middle Holocene assem-blages are in agreement with previous climatic reconstructions for the Sonoran Desert of summer temperatures greater than today, strong summer monsoons, and reduced winter rainfall (Van Deven-der et al. 1987; Van Devender 1990).

Previous Sonoran Desert midden studies inferred that more fre-quent freezes in the middle Holocene than today delayed the north-ward dispersal of important subtropical Sonoran Desert plants (Van Devender 1990). A number of trees and shrubs not found in the

Wolcott Peak middens are common near the sites today including *Cercidium microphyllum, Horsfordia newberryi, Hyptis emoryi, Larrea divaricata, Olneya tesota,* and *Simmondsia chinensis.* Their arrivals in the area or increases in abundance reflect late Holocene changes in the flora and vegetation in the last 4000 years.

Relict species. The modern climatic and vegetation regimes of Ragged Top were apparently established some time after 5000 years ago. The flora of Ragged Top is exceptionally rich for its elevation, size, and rock types. The richness is primarily due to a great variety of microhabitats allowing many species to live in a small area. The steep, shady cliffs and canyons also provide safe sites for relict populations extirpated from more exposed areas in the region. The packrat middens provide evidence that the Ragged Top relicts were isolated at different times. *Quercus turbinella, Vauquelinia californica,* and *Yucca baccata* are chaparral/woodland plants that were more widespread prior to 8900 years ago. Brown (1978) summarized isolated populations of relict plants including these species, *Juniperus erythrocarpa,* and *Rhus aromatica* in 22 desert mountain ranges in Arizona. A small population of *Ipomopsis multiflora* on Ragged Top may have been isolated at the same time. Other relictual populations of species that occurred more widely in the Wisconsin and are common in woodland and chaparral today include *Y. baccata* in the Silver Bell (3.5 km S) Mountains, *Agave deserti* and *Y. baccata* in the Waterman Mountains (10 km S), *Morus microphylla* (Texas mulberry), *R. aromatica, Q. turbinella, V. californica,* and *Y. baccata* in the Tucson Mountains (35 km SE), and *Agave palmeri* (Palmer agave), and *M. microphylla, Q. turbinella, V. californica* in the Picacho (35 km NNE) Mountains. We have seen no evidence of genetic changes in these populations after 9000 years of isolation.

Other Ragged Top relicts such as *Echinopepon wrightii* (wild balsam apple), *Ipomoea cristulata* Hallier f. (scarlet morning glory), and *Pisonia capitata* (Wats.) Standl. (garumbullo) are more topical, summer rainfall plants which probably reached the area between 4000 and 8900 years ago. The latter is a tropical shrub in the Nyctaginaceae disjunct from the nearest Sonoran populations by 460 kilometers (Wiens 1990). A single colony of four female plants is in a narrow, shady crevice. Other subtropical relicts whose dispersal and isolation probably dates to the middle or late Holocene include *Coursetia glandulosa* Gray (baby bonnets) on Pan Quemado (12 km SSE) and Ragged Top, and *Stenocereus thurberi* (Engelm.) Gibson & Horak on Desert Peak (34 km NE; Benson, 1982) and in the Roskruge Mountains (24 km S: 1.8 mi. NW Pescadero Mountain, T14S R9E S9, NW¼, 825 m elev.; S. Norman personal communication 1991). Pollen and seeds of *Bursera* in packrat middens record the arrivals of *Bursera* aff. *microphylla* (elephant tree) in the Wa-

terman Mountains by 5190 yr B.P. (Anderson and Van Devender 1991).

The middens also indicate that the abundances of plants in the modern desertscrub community on Wolcott Peak have increased and decreased, and local distributions have shifted in the last 5000 years. Studies of more continuous Holocene midden sequences from the Sonoran Desert suggest that community composition and structure have varied continuously without approaching equilibria in response to climate changes on time scales from millennia to decades (Van Devender et al. 1987; Anderson and Van Devender 1991; Van Devender 1990).

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NOTES

GALIUM REYNOLDSII EQUATED WITH *G. GALAPAGOENSE* WIGGINS.—Lauramay T. Dempster, Jepson Herbarium, University of California, Berkeley, CA 94720.

In 1980 (Allertonia 2(4), p. 255) I published *Galium reynoldsii,* based on two specimens housed at GH. One has the information "Andes, Capt. Reynolds," the other "S. Chili, T. G. Reynolds." No dates are given.

In 1971, nine years before the publication of *G. reynoldsii,* I saw on Floreana Island in the Galapagos, but did not collect, a very fine-textured *Galium* scrambling over shrubbery to a height of about four feet. Repeated attempts to have others collect this plant for me were finally successful when J. E. Lawesson sent me an excellent specimen, collected by him and associates in 1986. This, beyond all doubt, is identical with *G. reynoldsii* of Chile.

The most unusual character of this plant is its remote, solitary, outward-facing fruits, each opposite to a solitary leaf, except where branching occurs, the fruit then being subtended by two leaves. "The inflorescence should probably be interpreted as a series of extreme cymule reductions, each apparently axillary flower being in fact terminal" (Dempster 1980).

The relationship between the Floreana plant and *G. galapagoense* Wiggins (Madroño 20, p. 250. 1970) from Santa Cruz Island was not easily determined, since the type material (CAS) of *G. galapagoense* is very young and not abundant. Significantly, Wiggins remarked "This species is unlike any of the known species of *Galium* on the mainland of South America, particularly in that the dichasium has each terminal flower sessile between the subtending leaves, and with the slender branches of the next order of the inflorescence arising in the axils between the leaves and the terminal flower. . . . Occasionally one of the axillary branches in a dichasium fails to develop, and then the morphologically terminal flower appears to be axillary to a leaf borne on a straight branch." The latter situation is usual rather than occasional in material seen from Floreana Island and (presumably) Chile.

Although I have yet to see good mature material from Santa Cruz Island, *G. reynoldsii* Dempster (1980) and *G. galapagoense* Wiggins (1970) must be the same. The extraordinary distribution, if true, still needs to be explained.

Who was Reynolds? Barnhart (Biographical notes on botanists 3. 1965) mentions a William Reynolds who collected in southern Chile and Patagonia in 1837. Asa Gray (Reports of Wilkes Expedition p. 673. Proc. Amer. Philosophical Society 82, no. 5. 1940) dedicated his genus *Reynoldsia* "to J. N. Reynolds, Esq., who merits this commemoration for the unflagging zeal with which he urged upon our government the project of the South Sea Exploring Expedition, and also for having made, under trying circumstances, an interesting collection of dried plants in southern Chili, many years ago." Wilkes states (Wilkes, Narrative of the U.S. Exploring Expedition. 1852), "Previous to my arrival at Valparaiso, the naturalists and some officers on board the *Peacock* and *Relief* had made excursions into the interior. On my arrival, I allowed all those who could be spared, and were desirous of visiting Santiago, sufficient leave to make the trip. Several set out for that city, and some with a view of extending their journey to the Cordillera beyond."

Despite the plethora of initials (T. G., J. N. and William) it appears that the collector we are seeking was William Reynolds, listed (Wilkes, Exploring Expedition. 1858) among the officers and men of the U.S. Ship *Vincennes* as "Passed Mid" (N.B, he later became "Captain"). "Joined *Peacock,* 1839. . . ."

Could Reynolds have collected his specimens in the Galapagos instead of Chile? It seems not, since there is no record of the Wilkes Expedition's having been near the Galapagos. We must assume, therefore, that *G. galapagoense* occurs in Chile, somewhere in the neighborhood of Santiago, or that the plants were carelessly handled, and a serious error made.

For much of the historical material I owe thanks to Joseph Ewan, who interested himself in the problem, and entertained me in a significant way in his library at the Missouri Botanical Garden.

WHAT IS *ARISTIDA PERUVIANA*?—John R. Reeder, Herbarium, University of Arizona, Tucson, AZ 85721.

In 1975, A. A. Beetle (Phytologia 30:348) described, as a new species, *Aristida peruviana,* citing as the type *Mexia 4172* from Dept. Arequipa, Province Islay, Peru (UC). [The correct Mexia number is 4173, and this is acknowledged in a letter from Beetle attached to the holotype sheet.] He indicated that the nearest relative of his new species appeared to be *A. peninsularis* Hitchc., a taxon which has been treated as a synonym of *A. californica* var. *californica* by Gould & Moran (Memoirs of the San Diego Society of Natural History 12:99, 100, 1981), and also by Reeder & Felger (Madroño 36:189, 1989). *A. californica* is a member of section *Arthratherum,* characterized by having the apex of the lemma articulated with a distinct, twisted awn column. The awns and column separate from the lemma body at maturity.

In his original description, Beetle makes no mention of an awn column. There is, moreover, no discussion concerning how the new species differs from its presumed closest relative, but the following key is provided:

First glume 10 mm long, second glume 20 mm long, awns 4 to 5 cm long
                                                                    A. peninsularis Hitchc.
First glume 5–6 mm long, second glume 10 mm long, awns 1.5 to 3 cm long
                                                                    A. peruviana Beetle.

Recently Dra. Hilda Longi-Wagner sent me a specimen of *Aristida,* clearly a member of section *Arthratherum,* which had been collected in Peru. She remarked that this collection was especially interesting, since it apparently represented the first South American record of an *Aristida* belonging to that section. This was somewhat of a surprise because I was aware of *A. peruviana* Beetle. Although I had not seen the type, I assumed it was a member of section *Arthratherum* because the author had indicated that it was a close relative of *A. peninsularis.*

Hoping to clarify the problem outlined above, I requested from the University of California, Berkeley, the loan of Beetle's type, along with any other specimens he had annotated as *Aristida peruviana.* When the loan arrived, it included the holotype (*Mexia 4173*), along with three other collections (*Anderson 733, Hutchinson 502, and Weberbauer 6867*). The latter three had been cited by Beetle in his original description, and are therefore paratypes. It is of interest that all of the above specimens, including the holotype, had been named *A. adscensionis* prior to the time that Beetle annotated them as his new species, *A. peruviana.*

Examination of these specimens revealed that all of them, indeed, do represent *Aristida adscensionis* L. All are readily recognized as members of that species, although there is some variation among them, as is to be expected with samples of this variable taxon. The Mexia specimen had been determined by Ivan Johnston; Oscar Tovar had annotated the Hutchinson collection. There is no indication of who first had named the Anderson specimen. Regarding the Weberbauer sheet, it was named originally "*Aristida adscensionis* L. fa. *typica,*" perhaps by Weberbauer himself. Moreover, this same specimen was cited as *A. adscensionis* by Hitchcock (Contributions of the U.S. National Herbarium 24:404, 1927), and also, as noted by Beetle, under that same name by McBride (Publications of the Field Museum of Natural History, Botany Series 13:183, 1936).

It is difficult to understand how Beetle could have considered quite ordinary specimens of *Aristida adscensionis* (section *Aristida,* and type species of the genus and section) to represent an undescribed species of section *Arthratherum.* None of the specimens which Beetle cited has any suggestion of an awn column or articulation at the apex of the lemma, definitive characteristics for this latter section.

Included with the material received on loan from UC were a number of sheets of unnamed *Aristida* from South America. An interesting sidelight is that among them was another Anderson specimen from Peru, his no. *970.* The data are: "Peru: Lambayeque—30 kil. south of Chiclayo; 80 m. elev. Arid desert seldom seen with any vegetation. Single plants covering large area. 10 cm high. This is the southern limit of this grass. 2 May 1949." On a slip within a packet pasted to the specimen sheet is written in pencil "new species." As it turns out, the specimen represents *Aristida chiclayense* Tovar, and was cited by the author as a paratype (Publicaciones del Museo de Historia Natural "Javier Prado." Serie B. Botánica 32:11, 12, 1984).

Curiously, although *Aristida chiclayense* is clearly a member of section *Arthratherum,* Tovar does not mention this. Nevertheless, his description "columna de las aristas de 4.5–6 mm de largo" and his figure suggest strongly this alliance. The holotype of *A. chiclayense,* which was kindly lent by US, is a close match for *Anderson 970,* and was collected in about the same locality and on the same date.

Finally, it is ironical that the two Anderson specimens referred to above have the consecutive UC herbarium accession numbers M154595 and M154596. This suggests that they were put into the herbarium at the same time, and both should have been available to Beetle at the time he studied material which resulted in his description of *Aristida peruviana.* He cites *Anderson 733* (UC-M154595) as a paratype, but does not mention *Anderson 970* (UC-M154596). As indicated above, *733* (along with the holotype and other paratypes cited by Beetle) is actually *A. adscensionis* (section *Aristida*), whereas *970* is a member of section *Arthratherum* (a relative of *A. peninsularis = A. californica*). Had Beetle used *Anderson 970* as the type of his *A. peruviana* in 1975, that name would be the legitimate one for the species described nine years later by Tovar as *A. chiclayense.* An opportunity was missed, and the publication of *Aristida peruviana* Beetle, rather than being the legitimate name of a valid species, only adds one more synonym to the long list of those of *A. adscensionis* L.

NOTEWORTHY COLLECTIONS

ARIZONA

CRYPTANTHA GANDERI I.M. JOHNSTON (BORAGINACEAE). — Yuma Co., Cabeza Prieta National Wildlife Refuge, Pinta Sands East, dunes at edge of the lava flow, vicinity of 20°05'50"N, 113°27'W (Las Playas Quadrangle Arizona–Sonora, 7.5 minute series, provisional edition 1990), ca. 210 m, locally common spring ephemeral, sympatric with *Cryptantha angustifolia,* associated perennials *Croton californicus, Hilaria rigida, Stillingia linearifolia, Tiquilia palmeri,* and *Triteleiopsis palmeri, Harlan and Telewski 90* (21 March 1992, ARIZ).

Previous knowledge. The Gran Desierto region in northwestern Sonora (Felger, Synopsis of the Vascular Plants of Northwestern Sonora, Mexico, Ecologica, 1993; Johnston, Studies in the Boraginaceae XIII, Journal of the Arnold Arboretum 20: 375–402, 1939), Baja California south to the vicinity of Pozo Alemán and El Barril (Wiggins, Flora of Baja California, 1980), and southeastern California in San Diego Co. (Munz, A flora of southern California, 1974).

Significance. First record in Arizona. Apparently this plant had been collected previously in Arizona. I. M. Johnston (*in* Kearney & Peebles, Arizona Flora, 1951) reported that "plants resembling *C. barbigera* but with a solitary, smooth, very acuminate nutlet 3 mm long were collected in the Tule desert, Yuma Co. (Darrow in 1941)." This could only refer to *C. ganderi* but we have not been able to locate the specimen. The present collection from the same, or approximately the same, area confirms the presence of this species in Arizona.

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CALIFORNIA

CLARKIA MOSQUINII E. SMALL SSP. *MOSQUINII* (ONAGRACEAE). — Butte Co., along 4.8 km of Dark Canyon Road between 0.5 and 5.3 km south of Big Bend Road, T21N R4E sect. 2, 11, 12, T22N, R4E, sect. 35, elev. 305–575 m. Plants were observed at 10 sites along the full 6.2 km of Dark Canyon Road (between Highway 70 and Lake Oroville) and collections made at 8 of those sites. All sites were steep rocky banks of the road cut through shale bedrock, although plants were usually the most robust in the soil at the base of the cut. The sites face W to S to SE and are mostly open exposures. Surrounding vegetation is principally a mixed conifer forest of *Pinus sabiniana, P. ponderosa, Pseudotsuga menziesii,* and *Quercus chrysolepis*; ridge-tops are often dominated by *Arctostaphylos viscida,* while the drainage bottoms have some *Acer macrophyllum.* Openings of annual grassland also occur on some southerly facing slopes. The few associates of *C. mosquinii* include *Monardella sheltonii, Antirrhinum vexillo-calyculatum* ssp. *intermedium,* and *Streptanthus tortuosus* var. *suffrutescens.* One species particularly common on these road-cut banks, *Mimulus bifidus,* was not found with *C. mosquinii.* Three other species of *Clarkia* were found along Dark Canyon Road: *C. purpurea* ssp. *viminea* was very common on the side of Dark Canyon Road opposite the cut-banks; it was rarely growing with *C. mosquinii*; *C. unguiculata*

was collected at one site about 0.1 km S of the lowest *C. mosquinii* site; and *C. concinna* ssp. *concinna* was collected at one site 0.4 km south of the lowest *C. mosquinii* site. 7 May 1987, *Janeway 2029* (CHSC, CAS); 1 June 1991, *Janeway 3976* (CHSC), *Janeway 3977* (CHSC, CAS), *Janeway 3978* (CHSC, CAS, MO), *Janeway 3979* (CHSC, CAS), *Janeway 3980* (CHSC, LA), *Janeway 3982* (CHSC, CAS), *Janeway 3983* (CHSC, CAS), *Janeway 3985* (CHSC, CAS); identifications by Harlan Lewis, March 1992. The following seed collections have been deposited with the long-term seed storage facility at Rancho Santa Ana Botanic Garden by Harlan Lewis: 5 June 1992, *Janeway 4220, 4221*; 12 June 1992, *Janeway 4230, 4231*.

Previous knowledge. This taxon has been known only from the 1959 type collection from "along California State Highway 40 alternate, 3.7 mi southwest of entrance to Plumas National Forest" (*Mosquin 3335*). Dark Canyon Road, formerly Highway 40 alternate, is thought to be the type locality. Several searches have been conducted during the past 25 years to relocate *C. mosquinii* ssp. *mosquinii,* including some by Ernst Small, but have not been successful (H. Lewis, Rare Plant Status Report, California Native Plant Society, 1977; Smith and Berg, Inventory of Rare and Endangered Vascular Plants of California, Fourth Edition, California Native Plant Society, Sacramento, 1988).

Significance. Clarkia mosquinii ssp. *mosquinii* is presently on List 1A (Smith and Berg, Plants presumed extinct in California, California Native Plant Society, 1988) and is noted as "Presumed Extinct" in Hickman (The Jepson Manual, University of California Press, Berkeley, 1993). These collections reestablish the taxon as extant. One caveat is that although Harlan Lewis is "convinced" that these specimens are indeed *C. mosquinii* ssp. *mosquinii,* he urges that a chromosome count be taken to further confirm the identification; this species is the only one in the genus with six pairs of chromosomes.

CLARKIA MOSQUINII E. SMALL SSP. *XEROPHILA* E. SMALL (ONAGRACEAE).—Butte Co.: NE of Oroville, N of the French Creek Road crossing of Peavine Creek, T22N R6E sect. 30, elev. 650 m, roadside of decomposing granite in area of *Pinus ponderosa, Calocedrus decurrens, Quercus kelloggii,* 11 July 1981, *Schlising, Tarp & Banchero 4134* (CHSC); about 24 km NE of Oroville, about 3.2 km SE of intersection of the Oroville–Quincy Highway and Ponderosa Way, T20N R5E sect. 4, elev. 520 m, on dry, rocky, red soil along the road in region of foothill woodland, 26 June 1983, *Ahart 4118* (CHSC); at the little building at the Ponderosa Dam, about 3.2 air km NE of Forbestown, T20N R6E sect. 33, elev. 335 m, on damp granite soil in the disturbed cutbank, mixed conifer forest, 8 June 1984, *Ahart 4663* (CHSC). Identifications by Harlan Lewis, October 1992. Location and habitat information taken from the herbarium labels.

Previous knowledge. This taxon has been known only from the type collection (*Small 178*) and one other collection (*Mosquin 3336*), both from "along Highway, 0.2 mi west of Enterprise." This location was inundated by lake Oroville in 1968; the subspecies has not been reported since 1967 (Smith and Berg, 1988; Hickman 1993; citations in above Noteworthy Collection).

Significance. Clarkia mosquinii ssp. *xerophila* is presently on List 1A of Smith and Berg (1988) and is noted as "Presumed Extinct" in Hickman (1993). These collections reestablish the taxon as extant.

It was at the request of Vern Oswald that in October 1992 Harlan Lewis looked at all 58 collections of *Clarkia* section *Myxocarpa* at CHSC for misidentified specimens of *Clarkia mosquinii.* This resulted in the "discovery" of the three occurrences of *Clarkia mosquinii* ssp. *xerophila* reported above.

—LAWRENCE JANEWAY, Herbarium, Department of Biological Sciences, California State University, Chico 95929-0515.

MONARDELLA DOUGLASII BENTH. VAR. *VENOSA* (TORREY) JEPSON (LAMIACEAE).—
Butte Co., bottoms of canyons between Neal Road and Hamlin Canyon, ca. 8 km
SE of Chico, 2.4 km E of Highway 99, T21N R2E sect. 14 at 84–90 m. The six small
locations, containing from less than 10 to over 1000 plants each, are scattered within
a 60 ha area in two separate but interconnected canyons. Most of the plants are on
flat to gently sloping terrain, within 64 m of an intermittent stream channel in the
annual grassland component of a foothill woodland community. The plants are found
only in lenses of dark gray, deeply cracking clay within alluvium derived from the
upslope Tuscan Mudflow rock outcrops. The entire canyon area supporting this taxon
is actively grazed by cattle and sheep. Associated species: *Geranium dissectum, Centaurea solstitialis, Navarretia nigelliformis, N. heterandra, Hesperolinon californicum,
Vulpia* spp., *Evax caulescens, Trifolium hirtum, Brachypodium distachyon.* 9 May
1992, *Janeway and Castro 4162* (CHSC); 10 May 1992, *Castro and Janeway 456*
(CHSC); 16 May 1992, *Janeway and Castro 4187* (CHSC, CAS); 19 May 1992, *Castro
and Jokerst 457* (CHSC, CAS, DAV, UC); identification confirmed by J. D. Jokerst.

Previous knowledge. The most recent collection of *Monardella douglasii* var. *venosa*
was in 1935 from near Copperopolis in Tuolumne County (435 m) by J. A. Rutter
(UC); the taxon had not been collected since. There are only four other historical
collections: the type specimen collected in 1854 from "Plains of the Feather River,
near Marysville" by Bigelow, and three others, from "Cherokee, Butte County" by
Bidwell in 1879, from "Chico Valley" by Parry in 1882 (UC), and from "Chico" in
1883 (CAS) also by Parry (Taylor m.s. 1983, Flora Buttensis 4(1):35; label information
verified by B. Ertter personal communication 1993, and B. Bartholomew personal
communication 1993). A sixth historical collection in 1876 (UC), originally from the
Lemmon Herbarium, gives an incorrect location of "Crafton, San Bernar-
dino County" (annotation by J. Ewan 1934).

Significance. This distinctive taxon is presently on List 1A (Smith and Berg, Plants
presumed extinct in California, California Native Plant Society, 1988). These col-
lections reestablish the taxon as extant. These occurrences provide for habitat de-
scription; this information was omitted from labels on previous specimens, inhibiting
productive search for this presumed extinct plant.

The entire area in which all six patches of *M. douglasii* var. *venosa* was found was
burned in a wildfire on 25 Sept. 1992. Abundant seedlings were observed by the
principal author approximately four weeks later, following two rainstorms. These
seedlings showed only their two cotyledons; they were identified by smell and prox-
imity to last season's *Monardella* skeletons.

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MEXICO

LILIUM PARRYI S. WATSON (LILIACEAE).—Sonora, Sierra de los Ajos, Arroyo Fri-
jolito, vicinity of 30°57′N, 109°57′W (Carta Topografica, CETANAL, Cuquiarichi
HI2B54, 1974), ca. 2100 m. One highly localized population of 48 individuals (stems);
canyon bottom on edge of steep drop-off in dense shade of pine-oak woods with *Acer
grandidentatum, Abies concolor, Aralia racemosa, Smilacina racemosa, S. stellata,
Habenaria limosa, Thalictrum fendleri,* and *Malaxis ehrenbergii. Fishbein 734, Felger,
Garza, Haro, Malusa,* and *Turner* (9 October 1992, ARIZ, MEXU, MO, RSA, TEX,
UC). While standing in dim light in the late afternoon just prior to discovery of this
population, Fishbein remarked "This looks like lemon lily habitat," and Felger an-
swered "Like those behind you?"

Significance. First record for Mexico, the only member of the genus in Sonora.

Previously known from southern Arizona in the Huachuca and Santa Rita Mountains (S. Rutman, Handbook of Arizona's endangered, threatened, and candidate plants, U.S. Fish and Wildlife Service, Phoenix, AZ, 1992) and recently located in the Chiricahua Mountains (East Turkey Creek, 7400 ft, *Klay s.n.* (9 Jun 1992, ARIZ). Malusa, Warren & Gori, Population Studies of Sensitive Plants of the Coronado National Forest, Arizona, unpublished report, Arizona Nature Conservancy, Tucson, 1993), and also in southern California (Hickman, The Jepson Manual, University of California Press, Berkeley, 1993). Throughout its range this species is rare and narrowly restricted in distribution and in the U.S. has Category 2 status (a taxon for which the U.S. Fish and Wildlife Service has insufficient information to support a proposed rule to add the species to the threatened or endangered species list; Rutman 1992).

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RUMEX ORTHONEURUS RECH. F. (POLYGONACEAE).—Sonora, Sierra de los Ajos: Hoya del Packard, vicinity of 30°56′N, 109°58′W (Carta Topografica, CETANAL, Cuquiarichi HI2B54, 1974), ca. 2200 m. Five individuals observed in a narrow, steep canyon bottom with tall *Alnus oblongifolia, Pseudotsuga menziesii, Acer grandidentatum, Juglans major, Symphoricarpos oreophilus, Plantago major. Felger 92-908, Fishbein, Garza, & Haro* (10 October 1992, ARIZ, MEXU, UC, TEX). Arroyo Frijolito, vicinity of 30°56′N, 109°57′30″W, ca. 2450 m. Roughly 30 individuals observed in a dry canyon bottom below a seep with *Pinus strobiformis, Juniperus deppeana, Quercus gambelli, Rhamnus betulifolia, Acer grandidentatum, Euphorbia alta. Fishbein 698, Felger, Malusa, Turner, Garza, & Haro* (9 October 1992, ARIZ, MEXU).

Significance. First record for Mexico. Previously known only from low gradient streams at high elevations in southeastern Arizona where it is considered a Category 1 plant (a taxon for which the U.S. Fish and Wildlife Service has sufficient information on vulnerability and threats to support a proposal to list it as threatened or endangered). Seeds from Arizona plants were grown without difficulty in containers out-of-doors at the Arizona–Sonora Desert Museum in Tucson (Mark A. Dimmitt personal communication, 1993); these plants were successfully established in suitable habitats in the Chiricahua Mountains in southern Arizona (Malusa, Warren & Gori, Populations Studies of Sensitive Plants of the Coronado National Forest, Arizona, unpublished report, Arizona Nature Conservancy, Tucson, 1993).

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MONTANA

HALIMOLOBOS PERPLEXA (HEND.) ROLLINS (BRASSICACEAE).—Ravalli Co., Bitterroot Mountains, upper West Fork Bitterroot River drainage, ca. 1.6 k S of the confluence of Sheep Creek and the West Fork, on a steep SE-facing slope in loose, granitic gravelly loam soils, in a shrub-dominated community with *Ceanothus velutinus, Physocarpus malvaceus, Prunus virginiana, Salix scouleriana,* and *Symphoricarpos albus,* T4S R22W sect. 9 NW¼, 1865 m, 24 Jun 1992, *J. S. Shelly 1657* (MONT); same location, on a steep south-facing slope, with *Artemisia tridentata, Agropyron spicatum, Festuca idahoensis, Achillea millefolium, Eriogonum umbellatum, Balsa-*

morhiza sagittata, Koeleria cristata, Penstemon albertinus, Carex geyeri, and *Gilia tenerrima,* 27 Jun 1992, *J. S. Shelly 1660* (GH, ID, MONT, MONTU, MRC).

Significance. First records for Montana. This population represents a range extension for var. *lemhiensis* Hitchc., previously known only from the Salmon River drainage in Custer, Lemhi, and Valley cos., Idaho (Idaho Conservation Data Center, Boise). The plants are common in three subpopulations, and spread by long, thin rhizomes that are deep-seated in the loose soils.

HAPLOPAPPUS ABERRANS (A. NELS.) HALL (ASTERACEAE).—Ravalli Co., Bitterroot Mountains, in rock crevices and on short sandy and gravelly slopes, below and above cliffs, with *Sedum stenopetalum* and *Heuchera grossulariifolia,* T1N R22W sect. 14, 1463 m, 27 Aug 1989, *K. Lackschewitz 11618, W. Albert, and J. Hoy* (MONTU); Ravalli Co., West Fork Bitterroot River drainage, east of bitterroot National Forest Rd. 91, ca. 2 km N of Painted Rocks Lake Dam, ca. 32 air km SSW of Darby, ca. 80–100 plants growing in cracks at base of dry granite cliff, *Pinus ponderosa/Pseudotsuga menziesii* forest, with *Cercocarpus ledifolius, Penstemon diphyllus, P. fruticosus, Campanula rotundifolia, Woodsia scopulina,* and *Ribes cereum,* T1S R22W 23 center, 1463 m, 30 Jul 1990, *J. S. Shelly 1620, K. Lackschewitz, W. Albert, and K. McBride* (MONT, MRC).

Significance. First records for Montana. Previously known only from central Idaho.

LIPARIS LOESELII (L.) L. C. RICH. (ORCHIDACEAE).—Lake Co., all in the northern Swan River valley: "Porcupine Fen," 30 m W of USFS road 9719, 9.7 km SW of town of Swan lake, very local and scarce, saturated peatland (open patterned fen) dominated by *Carex interior, Carex rostrata, Eleocharis tenuis* and mosses, with shrub islands comprising *Betula glandulosa,* 2% slope, NE aspect, T24N R18W sect. 14 NW¼ NE¼, 957 m, 11 Jun 1992, *M. Mantas 490* (ID, MONTU); "Swan River Fen," NE of Flathead N.F. Rd. 9719, ca. 0.56 air km S of mouth of Porcupine Creek, 7.25 air km SSW of Swan Lake (town), in mossy, saturated peatland, with *Betula glandulosa, Salix candida, Carex lasiocarpa,* and *Picea engelmannii,* T24N R18W sect. 2 SW¼, 945 m, 13 Jun 1990, *J. S. Shelly 1615* (MONTU); same location as *Shelly 1615,* ca. 100–125 plants, 18 Jun 1992, *J. S. Shelly 1651 and S. Chadde* (MONT); "Lost Creek Fen," ca. 0.4 air km E of St. Hwy. 83, ca. 4.8 km S of Swan Lake (town), 110 plants counted, in a carr with *Betula glandulosa, Carex lasiocarpa, C. interior, C. cusickii, C. capillaris, C. aurea, C. dioica, Eriophorum viridicarinatum, Eleocharis tenuis, Picea engelmannii, Rhamnus alnifolia,* and *Epipactis gigantea,* T25N R18W 36 SE¼ NW¼, 966 m, 19 Jun 1992, *J. S. Shelly 1655 and S. Chadde* (MRC); "Plum Creek Fen," west side of Swan River valley, ca. 0.16 km W of Flathead N.F. Rd. 888, ca. 1.6 km S of junction with Rd. 9719, ca. 1.6 air km E of Woodward Point, ca. 16.1 air km S of Swan Lake (town), 76 plants counted, in moist to saturated peat of a well-developed fen, with *Betula glandulosa, Carex lasiocarpa, Eleocharis tenuis, Menyanthes trifoliata, Picea engelmannii,* and *Epipactis gigantea,* T23N R18W sect. 1 W½ NW¼, 1015 m, 14 Jul 1992, *J. S. Shelly 1670 and S. Chadde* (MONT); "Point Pleasant Fen," E side of St. Hwy. 83 across from Point Pleasant campground, 30 plants counted, in ecotone between open fen and adjacent forest, with *Carex lasiocarpa, C. flava, Lobelia kalmii, Scirpus acutus, Betula glandulosa, Juniperus communis,* and *Picea engelmannii,* T24N R17W sect. 19, 979 m, 14 Jul 1992, *J. S. Shelly 1679 and S. Chadde* (MONT).

Significance. First records for Montana. The only other known stations in the Pacific northwestern United States are in Klickitat and San Juan cos., Washington, where it is considered endangered (*Endangered, Threatened and Sensitive Vascular Plants of Washington,* Washington National Heritage Program, 1990). Otherwise known from Nova Scotia to Alabama, west sporadically to Saskatchewan, continental Northwest Territories and British Columbia (Straley et al., *The Rare Vascular Plants of British Columbia,* 1985), North Dakota and Iowa, and in Europe. All observed Montana

populations are small. The plants typically occur in semi-shaded carrs and fen-forest ecotones, or in full sun along water tracks flowing across the fens.

LYCOPODIUM INUNDATUM L. (LYCOPODIACEAE).—Missoula Co., Swan River valley, 0.56 air km W of Kraft Creek, 0.64 air km N of Flathead N.F. Rd. 9590, ca. 8.85 air km SSW of Condon, ca. 300–400 stems in scattered small patches, in organic crust of a basin fen, with *Carex lasiocarpa, C. Buxbaumii, Drosera anglica,* and *Dulichium arundinaceum,* T20N R17W sect. 28 NE¼ SE¼, 1253 m, 27 Jul 1988, *J. S. Shelly 1503* (MONTU, OSC).

Significance. Second report for Montana. Previously reported for "n.w. MT" (Hitchcock et al., *Vascular Plants of the PNW,* Part 1, 1969), but the basis for this is unknown. Recent floristic surveys of fens in northwestern Montana have not revealed any additional stations in the state. Interruptedly circumboreal, S in North America to NW California, Idaho, NW Montana, Minnesota, New York, and Virginia, and to Florida and Texas. We thank Klaus Lackschewitz for providing label data and encouraging publication of these records.

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NEW MEXICO

CRYPTANTHA GRACILIS OSTERH. (BORAGINACEAE).—San Juan Co., Animas River Breaks between Farmington and Aztec, T30N, R12W, S34, elev. 1740 m, 10 May 1982, *Fletcher 5941A* (UNM); 13 km NW of Aztec, T31N, R12W, sect. 16, on sandy clay beneath *Juniperus,* elev. 1800 m, 17 May 1983, *Sivinski 1078* (NMC, UNM); 26 km NE of Shiprock, T32N, R16W, sect. 19, common on sandy clay under *Juniperus,* elev. 1720 m, 17 May 1983, *Sivinski 1090* (UNM).

Significance. This species ranges from Oregon to northern Arizona. These are the first records for NM which represent a minor southeastern range extension from San Juan Co., Utah.

CRYPTANTHA RECURVATA COVILLE (BORAGINACEAE).—San Juan Co., Fruitland, T30, R15W, S24, shale hills, elev. 1645 m, 25 April 1979, *Marley 1797* (UNM); 4 km S of Chaco River on E side of the Hogback, T29N, R16W, sect. 28, on sandy soil, 29 April 1983, *Knight 2467* (UNM); 26 km NE of Shiprock, T32N, R16W, sect. 19, common on sandy lenses in sandstone outcrops, elev. 1720 m, 17 May 1983 *Sivinski 1091* (UNM).

Significance. This species ranges from Oregon to southern California to western Colorado. These are the first records for NM which represent a minor southeastern range extension from San Juan Co., Utah.

EPIPACTIS HELLEBORINE (L.) CRANTZ. (ORCHIDACEAE).—Bernalillo Co., Rio Grande River at the City of Albuquerque, Rio Grande Nature Center, occasional in dry understory leaf litter beneath a riparian, deciduous forest of *Populus fremontii* var. *wislizenii* Wats. and *Elaeagnus angustifolia* L., 26 June 1990, *Sivinski & Cully 1510* (UNM).

Significance. An introduced European species that is becoming well established in the eastern forests and western coastal woodlands of North America. This is the first record for NM and the arid southwestern states.

HELIANTHUS PARADOXUS HEISER (ASTERACEAE).—Chaves Co., Bitter Lake National Wildlife Refuge, 8 km NE of Roswell, T10S, R25E, sects 4, 9, 10, 15, 16, 20, 21, 28 and 29, common along the riparian edges of ponds within the refuge, elev. 1060 m, 11 September 1991, *Sivinski 1813* (UNM); Guadalupe Co., Santa Rosa, T8N, R21E, Sections 2, 10, 11, 12 and 14, common on numerous springs, seeps and pond riparian areas, elev. 1390 m, 25 September 1992, *Sivinski 2066* (NMC, UNM).

Significance. Martin and Hutchins did not include this species in A Flora of New Mexico (vol. 2, 1980) even though Heiser (Rhodora 60:272–274, 1958) identified an 1851, Valencia Co., NM specimen as belonging to this species. Its New mexico residency was firmly established when it was discovered near Dexter in Chaves Co. (Seiler et al., SW Natur. 26:431, 1981). This plant has recently been considered a category 1 candidate for listing under the federal Endangered Species Act. These new locations greatly improve its probability of survival since the Bitter Lake location is within a national wildlife refuge and many of the plants at Santa Rosa occur in municipal fishing parks. The range of this sunflower in the Pecos River drainage is also extended 140 km to the north.

OXYTROPIS DEFLEXA (PALL.) DC. VAR. *DEFLEXA* (FABACEAE).—Rio Arriba Co., Cañon de los Alamos, 7 km N of La Madera, T26N, R8E, sect. 25, SW¼, canyon bottom in ponderosa pine forest, elev. 2280 m, 26 July 1991, *Sivinski & Lightfoot 1769* (NMC); same location, 30 July 1992, *Sivinski 1929* (UNM). Determination made by Dr. Richard Spellenberg.

Significance. Martin and Hutchins include this variation in A Flora of New Mexico (vol. 1, 1980) as "probably" in the northern part of the state with no certain records. This is the first vouchered record of this plant for NM and a minor range extension from the mountains of southern Colorado.

PHACELIA CEPHALOTES A. GRAY (HYDROPHYLLACEAE).—McKinley Co., Zuni Mts., Six-mile Canyon, T14S, R15W, sect. 7, SW¼, occasional on dark shale with *Juniperus* and *Sarcobatus,* elev. 2180 m, 31 May 1992, *Sivinski 1871* (NMC, UNM).

Significance. First record for NM and a minor range extension to the east from adjacent Apache Co., Arizona.

PLANTAGO ELONGATA PURSH SUBSP. *ELONGATA* (PLANTAGINACEAE).—San Juan Co., 1 km E of the Los Pinos Arm of Navajo Reservoir, T32N, R7W, sect. 20, NW¼, rare on sodic, sandy shale outcrops with strong smell of selenium, piñon-juniper woodland, elev. 1900 m, 9 May 1991, *Sivinski & Lightfoot 1658* (UNM).

Significance. First record for NM and a southern range extension of 200 km from the nearest published location in western Colorado. This collection confirms Bassett's (Canadian Journal of Botany 44:468–469, 1966) expectation that this widespread species would be found in NM.

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REVIEWS

Fire in South African mountain fynbos. Ecosystem, community and species response at Swartboskloof. Edited by B. W. VAN WILGEN, D. M. RICHARDSON, F. J. KRUGER, H. J. VAN HENSBERGEN. 1992. Springer-Verlag, New York, Berlin, Heidelberg. xxi + 325 pages. $138, ISBN 0-387-53301.

Cursed by the difficulty of replication at the large scale that the study of many important questions demands, ecologists must of necessity look to independent studies in systems with similar properties for confirmation or refutation of hypotheses. For this reason at least, ecologists of the Pacific slope will find this book valuable. It reports the results of a multi-investigator long-term study on the effects of fire on the 373 ha Swartboskloof catchment in the Jonkershoek Valley near Cape Town. The site is dominated by fynbos, the species-rich analog of chaparral. Though different in many ways from chaparral, it is similar in the importance of fire to ecosystem processes. Like oak woodland, the forest that occurs at the site is restricted to narrow bands along the larger drainages.

The purpose of the study was to understand how fire affects processes in the catchment landscape at the population, community, and ecosystems levels. The research design was straightforward. Studies began well in advance of a management burn conducted in 1987 and for the most part the analyses involve before and after comparisons and careful description of post-fire recovery. Experimental manipulation was also used in moderation, for example exclusion plots in a herbivory study, and cutting treatments to explore the stimulus for flowering by geophytes; but this is not the place to look for innovative approaches for whole ecosystem manipulative experimentation.

Coverage is thorough. Three introductory chapters describe the topography, geology, climate, and biota, including an entire chapter on fuel properties, as befits a book centering on fire. These chapters, plus accompanying pictures, provide a good introduction to those unfamiliar with fynbos. Subsequent chapters consider forest-fynbos relations, coexistence and comparative life history and physiology of post-fire seeding and sprouting shrubs, fire stimulated geophytes (*Watsonia*), the exotic invasion of fynbos, the effect of small mammals, aspects of ant ecology, sediment yield and non-wettability, chemical budgets, soil microorganisms, and a final summary.

Students of fire-prone ecosystems and particularly of Mediterranean vegetation, will find much of interest in the volume, as will those concerned with how catastrophic events determine ecosystem properties. One conclusion is that catastrophe does not always mean drastic change. The fire had little effect on the overall catchment nutrient budget and sediment production. Before and after comparisons (using statistical methods some would criticize) showed a large increase only for potassium, a small increase for nitrate, and no change for all other ions measured. The authors attribute this to rapid uptake by resprouting shrubs and the filtering effect of the forest vegetation that lines the larger drainages. Microbial populations, though initially depleted by the burn, also recovered rapidly.

In contrast, change wrought by fire is the cornerstone of the argument made by Richardson and Cowling to explain the susceptibility of fynbos to invasion by exotic woody species, particularly Australian *Acacia* and *Hakea,* and California and Mediterranean pines. They believe that the populations of native fynbos shrubs fluctuate in response to variation in fire timing and intensity. They argue that in pristine vegetation, there is coexistence mediated by stochastic variation. Fire-related crashes of local populations create windows of opportunity that are exploited by the expansion of competing populations and the temporary invasion of more dispersible natives. The exotics violate the rules of this stochastic game because unlike natives, they are

both readily dispersed and less subject to local extinction because of vegetative vigor, early age at first reproduction, and high seed production. They hypothesize a kind of ratcheting effect in which the less variable populations of invaders expand at the expense of the more variable natives.

A specific case of coexistence that continues to intrigue ecologists is the coexistence of sprouting and non-sprouting shrub populations. The basic problem is to explain why the sprouters that hold their ground don't exclude those dependent on seeds. The problem is explored in detail in two chapters. The idea that there are counter-balancing advantages is an obvious general explanation. The Swartboskloof studies both support and refute particular aspects of this theory. Contrary to the expectations of some, Smith et al. failed to find that the two groups of species differed significantly in physiological traits. But they also found that within Swartboskloof the dominance of sprouting species increased with increasing soil moisture. The same mixed bag of affirmations and refutations resulted from comparisons of two species of sprouting and non-sprouting *Protea* species. As predicted from allocation theory (and common sense), the seeder established significantly more seedlings per parent plant. In common with similar chaparral intergeneric comparisons, they found that adult mortality was lower and decreased with age in the sprouter, whereas mortality was higher and tended to increase with age in the seeder. Surprisingly, no differences were found in seedling mortality. Overall though, the importance of catastrophe in explaining coexistence was supported by the conclusion that seeders overcame the greater longevity of the sprouters because of a greater capacity for population expansion after the fire.

The dominance of shrubs on the site is an anomaly that gets considerable attention. With 1500 mm precipitation, tree-dominated vegetation would be expected. Data presented make a convincing case that forest species can establish and grow in fynbos. But forest species are more sensitive to fire and less able exploit post-fire conditions, thus leading to the conclusion that fire is the primary factor preventing a succession toward forest.

This combination of interesting natural history with frequent allusions to data from other regions is a strength of the book. Students of Mediterranean ecosystems in particular will find it of interest. Together with the recently published "Ecology of fynbos" (Oxford University Press, Cape Town, R. M. Cowling, Ed.) we have an excellent summary of current knowledge against which to test the generality of our ideas about the function of Mediterranean-climate shrublands.

Finally I have a mundane but important criticism relevant to resilience, not of ecosystems, but of the book itself. Even before this review was complete page 275 had fallen out of my copy and page 179 clung by less than a cm. We expect our second-hand Barbara Cartland paperbacks to do this, but a new and pricey Springer hardback should be better able to take abuse.

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Note: I have learned that Springer has rebound all remaining copies; therefore books purchased after this review appears should be sound.

The Jepson Manual: Higher Plants of California. By James C. Hickman (ed.). 1993. University of California Press, Berkeley. xvii + 1400 pages. ISBN 0-520-08255-9.

With over 5800 vascular plant species growing outside cultivation, California has the most diverse flora of any state—perhaps even any floristic region—in the U.S. Preparing a manual for such a large flora is a monumental task. Making that manual useful not only for professional botanists but for virtually anyone with a serious interest in plants may seem impossible. That, however, is just what the team at the Jepson Herbarium, led by the late Jim Hickman and Larry Heckard, has attempted. They succeeded remarkably well.

The editorial team took several steps to promote the accessibility of the manual. Perhaps the most controversial of these was to strictly limit the technical vocabulary. Though this decision must have caused untold frustration to contributors and editors alike, the reduced jargon is effective and refreshing. The main drawback is an occasional decrease in brevity. A well-written glossary, cross-referenced and extensively illustrated, enables even the novice to use the many specialized terms still required. The glossary would, however, have been better placed immediately before the index or in another easily found place rather than buried in the introductory text.

The extensive use of illustrations is exemplary and further improves the book's accessibility. Nearly every genus is shown, usually by several species that are commonly encountered or show diagnostic or hard-to-describe features. The drawings, executed primarily by Emily Reid and Linda Ann Vorobik, are outstanding. I have found that the illustrations often allow me to forgo confirming my determinations with herbarium specimens. For those without access to herbarium specimens, the illustrations will prove an effective substitute.

Keys can make or break a floristic manual. Nearly all the keys in the *Jepson Manual* are very good. Some are quite innovative, departing in style and content from previously published keys for those taxa. Most striking are the extensive efforts made to key out variable taxa in more than one place. The family key, prepared by David Keil, is particularly notable in this regard, and in allowing for common misinterpretations. It is a joy to use. Even inexperienced botanists will have little difficulty identifying plants to family. Also noteworthy are the keys for several large families, including the Asteraceae and the Poaceae. The key to the former, also a Keil product, is more usable than any others for this family I have seen. I found the key to Poaceae by James P. Smith, Jr., less successful. The second couplet attempts to simplify the problem of interpreting inflorescence structure by asking whether the inflorescence branches are "easily seen at arm's length." This probably is not too bad once one gets over the embarrassment of holding the plant that way. Unfortunately, the key does not allow for many exceptions to or misinterpretations of this early couplet. As a colleague pointed out to me, the abundant weed *Bromus madritensis* var. *rubens,* which usually has an obscurely branched inflorescence, will be very difficult to key to genus. He also noted that many depauperate annual grasses, e.g., several *Bromus* species, have only one spikelet and so will key to *Danthonia unispicata.* In some other keys, attempts at brevity led to awkwardness, for example the first couplet in Scrophulariaceae. Still, the *Jepson Manual* keys are among the best I have used.

Perhaps nothing in a manual stirs more controversy than its taxonomic treatments. With over 200 contributors, considerable variation could be expected. The editors deserve praise for their remarkably successful attempts at imposing uniformity of style. They had less control over content. Some treatments are innovative and reflect extensive work by taxonomic specialists or by experienced botanists whom the editors describe as approaching their work "as taxonomic authors for the first time." Others appear merely to have been taken from Munz's *California Flora* (1959; supplement 1968) and rewritten in the *Jepson Manual* style. Particularly disturbing is the small number of contributors who studied specimens, even from the major California herbaria (*fide* the staff at those institutions). I also found several examples where pertinent literature was overlooked. As a consequence of these problems, many taxonomic treatments—only time will show which—are not definitive.

Despite the great number of contributors, species concepts are almost consistently very conservative, resulting in extensive "lumping" (name changes from Munz's *California Flora* are listed in an appendix). Though nowhere in the book itself can I find a statement of taxonomic philosophy (an unfortunate omission), the contributors' guide directed authors to promote accessibility by ignoring minor variation and hard-to-see characters. That this conservatism was imposed by the editors is further shown by several contributors who have already published papers recognizing taxa they synonymized in the *Manual.* The consequences of this conservative approach for biological conservation are extensively discussed by Skinner and Ertter (*Fremontia*

22(3):23–27, 1993). Taxonomically its consequence should be a healthy stimulus for further research.

Much to the editors' credit, the taxonomic descriptions are remarkably consistent in organization. Many manuals and other taxonomic works have not stressed consistency, causing confusion and frustration. Besides morphology, species descriptions include abbreviated synonymy, chromosome numbers, distribution, toxicity, weediness, and horticultural value. Inclusion of the latter is particularly welcome given the tremendous interest in the use of native plants for drought-tolerant landscaping.

Unlike most manuals that give distribution by political units, the *Jepson Manual* uses biogeographic subdivisions. The 50 units are briefly described in the introduction and nicely mapped (in color) there and again on both inside covers. Almost exclusive use of biogeographic units is generally effective. Sometimes, though, it conveys a broader distribution than is accurate, particularly for narrowly distributed plants that are found in only part of a large unit. For example, *Aralia californica* is stated to be found throughout the California Floristic Province, which extends from northwestern Baja California to southwestern Oregon. *A. californica* actually reaches its southern limit in Orange County. Using biogeographic subdivisions also requires that authors and editors be familiar with the limits of these units throughout the state. Judging by the number of plants limited to the coastal regions of southern California that are reported in the *Manual* to grow in the Peninsular Ranges, this was not always the case. I also found several examples of plants known from the Peninsular Ranges but not listed from there in the *Manual*. Clearly the distributional information should not be taken too literally.

Even experienced botanists will be struck by the extensive use of abbreviations in the keys and descriptions, a consequence of dealing with California's diverse flora in a single volume. Though the abbreviations are nicely explained in a table, it is buried in the *Manual's* introduction. The table should have been reproduced inside one of the covers, and the geographic subdivision map shown only twice.

Discussions of California's geological history (by Jeffrey P. Schaffer) and the evolution of the state's distinctive climate and flora (by Dieter Wilken) provide valuable insights. Both include much recent evidence and are free of outdated community concepts. The introduction also includes a refreshingly unpedantic discussion of the pronunciation of scientific names.

The book has a clean layout and is very pleasing to the eye. Compactness, however, suffered; measuring 21.5 × 28 × 5.5 cm and weighing almost 2.5 kg, the tome stretches the term "field manual." Fortunately given its size and weight, the book seems well made. For a publication of its length and complexity, typographic errors are few and mostly insignificant. At least three will cause confusion, however. On page 23, lead 23 should result in *Swertia* not *Frasera,* which is not recognized in the generic treatment of Gentianaceae. According to David Keil, in his key to the Asteraceae, lead 35 on page 181 should give *Microseris douglasii,* and lead 24 on page 182 should give *Madia.* In addition, Balsaminaceae were left out entirely. The *Jepson Globe,* the newsletter of the Jepson Herbarium (individual subscriptions $25/yr payable to the Friends of the Jepson Herbarium, mailed to Jepson Herbarium, University of California, Berkeley, CA 94720), will publish errata quarterly and invites input.

Hickman and his team did a remarkably good job of making the complex and diverse California flora accessible. In presentation the *Jepson Manual* represents what a modern flora should be. Though its content may be uneven, it provides new insights into many groups and at the worst should stimulate further research. I recommend the book to anyone, from professional botanist to weekend plant enthusiast, who wants to learn more about California's diverse flora.

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OBITUARY

WALTER EMIL WESTMAN
(1945–1991)

The field of Mediterranean-ecosystem science lost a significant researcher, intellectual force, and personal friend with the untimely death of Walter Emil Westman on January 3, 1991. Walt died at the age of 45 from complications associated with AIDS. Over the two decades of his professional career, he made significant contributions to the fields of plant ecology, ecosystem science, and biogeography and environmental policy. He was the author of two books and nearly 100 articles over this too brief period. Among Mediterranean-ecosystem researchers, Walt is best known for his series of studies on coastal sage scrub communities in California and Baja California and on his work with plant community resilience to fire or pollutant stress. He was a leader in these studies in the application of multivariate approaches to understanding community level patterns. Equally significant, however, were his contributions in environmental policy and ecological impact research. His 1985 book, *Ecology, Impact Assessment, and Environmental Planning* was a pioneering and successful effort to integrate theoretical ecological principle with policy issues of environmental impact assessment and resource management.

Walt was born in New York City on November 5, 1945, and obtained his bachelor's degree in botany from Swarthmore College in 1966. He completed a master's degree in 1969 at Macquarie University in Australia, working with studies of the community ecology of eucalypt forests. This interest in quantitative approaches to community and ecosystem ecology led him to Cornell University where he completed his Ph.D. degree in 1971 working with the late R. H. Whittaker. His dissertation work on the structure and function of the pygmy forest ecosystem in the wet coastal forests of northwestern California have become a classic study on the edaphic control of ecosystem processes along catenas of soil change.

After completion of his Ph.D., Walt followed up his interest in applied ecology with a year in Washington, DC on a Congressional fellowship from the American Political Science Association. He served as a staff advisor to Senator Edward Muskie on the U.S. Senate Subcommittee on Air and Water Pollution, where he helped to write the important Federal Water Pollution Control Act of 1972. This experience was instrumental in developing his concepts of how science and public policy could be linked to bring a more quantitative approach to enlightened management of natural resources and realistic controls of air and water pollutants.

Walt returned to Australia for two years in 1972 where he was Lecturer in Ecology at the University of Queensland in Brisbane. This period was a productive one for research on biomass, productivity and nutrient cycling in subtropical eucalypt forests, with ten papers on this work published between 1975 and 1981. Walt returned to the U.S. in 1975 to take a faculty position at UCLA where he began his important work on coastal sage scrub ecosystems. In numerous publications, beginning in 1979 and continuing up to the present, he and his students developed a multi-disciplinary approach to vegetation sciences. This work ranged from biogeography, diversity and conservation biology to succession and community structure, to ecosystem stability and resilience in response, and to human impacts from fire and air pollution. Walt left UCLA in 1984, but continued an active interest in coastal sage scrub ecology. At the time of his death, he was staff scientist in Ecology and Environmental Policy at the Lawrence Berkeley Laboratory at the University of California, Berkeley.

Plant ecology was always a coequal interest with environmental policy for Walt Westman, and his contributions to this later field were particularly significant. Ecologists less familiar with this aspect of his career should look at not only his 1985 book, but a number of influential articles on this subject. Particularly notable are his "How much are Nature's services worth?" (Science 197:960–964, 1977), "Measuring the inertia and resilience of ecosystems" (Bioscience 28:705–710, 1978), "Managing for biodiversity: unresolved science and policy questions" (Bioscience 28:26–33, 1990),

and "Park management of exotic plant species: problems and issues" (Conservation Biology 3:251–260, 1990). With his remarkable level of energy, Walt freely gave his time to serve on advisory committees to numerous government agencies concerned with issues of environmental quality and resource utilization. These included the U.S. Senate Subcommittee on Environmental Pollution (1975–1976), the Global 2000 Study of the Council on Environmental Quality (1977–1978), the Commission on Ecology of the International Union for the Conservation of Nature and Natural Resources (1979–1991), the Ecosystem Effects Working Group of the EPA National Acid Deposition Assessment Program (chair 1985), and the Unmanaged Lands working Group of the United Nations Intergovernmental Panel on Climate Change (chair 1989–1991).

Beyond his scientific accomplishments, Walt was an accomplished classical violinist with training at the Julliard School of Music in New York City. Writing under a pseudonym, he had also published a number of short stories and poems. Social and ethical issues also formed an important part of Walt's life. In 1980, he became the founder and coordinator of the *National Organization of Gay and Lesbian Scientists and Technical Professionals,* and he was a participant in the *Gay and Lesbian History Project* in San Francisco. Until the time of his death, he was an active supporter of *Project Inform,* an advice and advocacy group for persons with AIDS.

Beyond the tangible scientific contributions made by Walt Westman during his life, his influence will be felt for many years through the career of the many students who worked with him during his years at UCLA. He was a stimulating and inspirational teacher, an interactive colleague, and a friend to many ecologists. His passing is especially untimely in light of the current Natural Community Conservation Planning process by the Resource Agency of California for the endangered sage scrub community—a process to which he would have contributed enormously. In 1981 he alerted ecologists to sage scrub's conservation crisis in his "Diversity relations and succession in Californian coastal scrub" (Ecology 62:170–184). His death is an irreplaceable loss to Mediterranean-ecosystem studies and the broader field of ecology as well.

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—PHILIP W. RUNDEL, Department of Biology and Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles, CA 90024; JOHN F. O'LEARY, Department of Geography, San Diego State University, San Diego, CA 92182; and GEORGE P. MALANSON, Department of Geography, University of Iowa, Iowa City, IA 52242

COMMENTARY

POINTS OF VIEW: DOES ENDANGERED
CHORIZANTHE VALIDA DO BETTER WITH GRAZING?

As a former investigator of environmental plasticity and population characteristics of rare and common annual plants under differing conditions (e.g., Hickman, Journal of Ecology 63:689–701, 1975 and 65:317–326, 1977), and because *Chorizanthe valida* S. Watson is such a sensitive taxon, I feel the need to respond to Davis and Sherman (Madroño 39:271–280, 1992).

I am in strong sympathy with detailed studies of endangered plants. Although I believe that Davis and Sherman's findings can be considered suggestive, they have not yet shown clearly that livestock grazing provides "a positive influence on the perpetuation of a rare, endemic plant" (Abstract, p. 271). The problem resides in interpreting the population feature they measured and in variables not addressed.

Green-plant density was the only population parameter measured in Davis and Sherman's study. It was emphasized at the urging of state and federal agencies (Davis and Sherman personal communication 1992). Unfortunately, density alone is an unreliable indicator of population success in plastic annuals (as it is in unthinned forest stands). I have confirmed repeatedly in annuals that the highest densities and ± uniformly small size are found in the most marginal environments. Some tiny, highly stressed annuals have had densities exceeding 30,000/m², but density was in no way a predictor of their "success."

Small, dense plants from grazed plots are shown in Davis and Sherman's Figure 3A. They set few seeds per individual and fit the general pattern produced by greater stress from some environmental factor. I deduce that they were unable to grow large enough to experience much competition for light or water.

The plant in Figure 3B (from a grazing exclosure) is robust and produced many seeds, as is expected under more benign physical conditions, and with moderate competition. The illustrated plants strongly suggest (against Davis and Sherman's assertion) that *C. valida* is a reasonable competitor. Furthermore, Davis and Sherman (personal communication 1992) suggested (from Bodega Bay rainfall data) that *C. valida* had done better in wetter years, under lusher conditions.

In 1989, individual plants in exclosures did much better than those outside: they have been estimated by Davis and Sherman (personal communication 1992) (and by me from information in their paper) to have set 6–10 times more seeds per unit area, despite their initial and continuing significantly lower density. Relative sizes were more or less comparable in 1991 (Davis and Sherman personal communication 1992), when ungrazed density was only 4% that of grazed, yet seed production was about half that of the grazed plots.

I have claimed that an annual plant is a seed's way of making more seeds—seeds and their dynamics are the greatly predominant part of the annual life cycle. Seed production is of much more importance to the success of annuals than is density.

Annuals have seed-storage mechanisms of various sorts. (Davis and Sherman [personal communication 1992] found germination to be difficult under greenhouse conditions, which is expected if there is seed storage.) This is compatible with the accepted advantages of the annual habit in marginal and unpredictable environments. One consequence of seed storage is that green-plant density sometimes has little to do with the numbers of seeds produced the previous year. Years of zero establishment can be followed by years of high green-plant density from stored seeds (fire annuals are a spectacular example).

Seed fates (as well as numbers) are thus of critical importance, however difficult

they are to study. Seeds were produced by virtually all (even tiny) green plants each year, which is in line with other observations. In ungrazed plots, either 1) a higher proportion of seeds died before green-plant establishment or 2) more seeds were stored in the soil, possibly timed variably for germination ("bet-hedging" against bad years) or awaiting growing seasons with favorable conditions. Alternative 2) might well be best for perpetuating the species, so some answer to the seed-fate question is needed before Davis and Sherman's primary conclusion is justified.

If the higher density in grazed plots were simply due to reduction of competition by grazing, these plants would not be so small. The question of why they were is not easily answered, but the fact does indicate a harsher environment. As they are avoided by cattle, grazing is not directly responsible. However, trampling by cattle in such sandy soils is almost certain to cause root breakage, decreasing water and nutrient availability.

If the precipitous density crash in ungrazed plots in 1990 were due to competition from palatable or perennial plants inside the exclosures, the significant rebound of 1991 would be unlikely. The crash in 1990 could have been caused by seed-storage vagaries or by abnormally high but undetected mortality of pre-establishment seedlings. Mortality patterns of germinants also need study.

These unresolved issues are caveats to Davis and Sherman's primary conclusion that grazing helps *Chorizanthe valida*. In fact, the information they presented may be interpreted as indicating that the opposite conclusion is correct. Until more data are available, especially concerning seeds and their fates, basing a management plan on their conclusion would be unwise.

Plant population dynamics is an inherently difficult area of study; nevertheless, it is the only way to understand what helps or hurts a population through time. Thought must be given to, and care must be taken in, measuring those features that are of most importance to the population under study conditions. Research sponsors and funding agencies for rare plant studies should be made aware that simplistic study requirements may eventually prove deleterious or even disastrous to the subjects of study.

I thank Liam H. Davis and Robert J. Sherman for their helpful critique of an earlier draft.

—James C. Hickman (deceased), 925 Corbett Avenue #204, San Francisco, CA 94131–1502.

ANNOUNCEMENT

Beginning 1 January 1994, all new manuscripts and correspondence concerning previously submitted manuscripts should be addressed to the new editor:

Dr. Robert Patterson
Department of Biology
San Francisco State University
San Francisco, California 94132

RESPONSE TO HICKMAN'S COMMENTARY

We appreciate the opportunity to respond to James C. Hickman's comments regarding our paper (Madroño 39:271–280, 1992) which we submitted with the hope that it would stimulate further research on *Chorizanthe valida* S. Watson and the management issues associated with grazing.

When we began this study, we were concerned that grazing by cattle might have a negative impact on *C. valida* and that successful management would require elimination of grazing. As our field observations progressed we came to a different point of view because populations declined in our exclosures and we were successful in establishing *C. valida* under grazing conditions (Table 2). In fact, our unpublished data for 1992 indicate that one of the introduction plots (Plot Y) now has 443 plants on the original 2 × 2 m plot with an additional 316 plants outside the introduction plot. Thus, not only has the existing colony been perpetuated for over a century under a cattle grazing regime, but at least one new colony was established and is expanding in the presence of grazing.

Hickman raises many issues, but these points are raised as applicable to *C. valida* with no supporting data. In fact, the Jepson Manual section on Chorizanthe, authored by Hickman, states *C. valida* is "threatened by cattle," again with no supporting data. We are more inclined to agree with Stebbins assessment of the genus as a "pioneer on xeric sites where little or no competition with other plants would occur." Grazing, as practiced on the existing colony, favors the maintenance of open, xeric sites with reduced competition.

We would certainly agree that more research is needed regarding seed production, but low densities are of concern. On eight of the 16 non-grazed sub-plots, *C. valida* reproduction failed entirely and on two of the sub-plots there was only one *C. valida*. The only reason the summary values for the exclosures reached the reported level, is that one of the exclosure plots (four sub-plots) still had 51 plants.

Seed success is apparently greater on grazed than on non-grazed plots. The seed yield from the non-grazed plots in 1989 could easily be 45,000 seeds/m^2. Of that number only 8/m^2 (0.02%) grew to maturity. A few meters away, on the grazed plots the seed yield was about 8000 seeds/m^2 and 228/m^2 (2.8%) grew to maturity. The grazed plots were on the same soil type and were subjected to the same weather conditions. Introduction plots (Table 2) give information consistent with that from the established grazed plots. The summer of 1989 counts for the introduction plots indicate successful seedling establishment values of approximately 3.8%, 2.2% and 9.8% under grazing treatment.

We are not aware of seed-bank studies on this species. Hickman suggests that since there was low density on the ungrazed plots, there is probably considerable seed storage. Liam Davis grew *C. valida* under greenhouse conditions in an attempt to develop information regarding germination and seedling survival. Hickman misinterpreted our communication on this topic by stating that we found germination to be difficult. Survival rates were low, but germination in vitro was approximately 80%.

Hickman states that small stature indicates a harsher environment (trampling). We have seen no evidence in the field to support that assumption. We did not anticipate the plasticity of *C. valida*, so no size measurements were taken and we don't know why the plants in the grazed area are smaller. Figure 3A typifies *C. valida* in the grazed plots and we did not observe any obvious changes in the uniformly small stature of these plants over five years. Other collections from this grazed colony (Howell 1980 CAS) demonstrate comparable size. We suspect the difference in stature is due to the effect of shade on the non-grazed sites. Greenhouse studies may answer this question.

Hickman also states that high numbers of an annual indicate that the study area must be a marginal (stressful) environment. In his correspondence he suggested that the "significant rebound" in the exclosures from 1990 to 1991 might be due to *C. valida* competing "less well under lusher conditions." This is consistent with his premise, but not consistent with our unpublished observations. If anything, our data suggest that *C. valida* does better under wetter conditions, but our entire study occurred during the 1986–1992 drought.

With regard to management, our concern is that managers are more inclined to respond to recognition of responsibility for an endangered plant by rushing to remove grazing. We have personally observed declines in populations of *Blennosperma bakeri* Heiser following its recognition as endangered and its subsequent "protection" from grazing. Range managers recognize that many annual herbs survive in pasturelands only because potential competitive species that might overtop them are held in check by grazing. Also, there are many coastal pasturelands where *Baccharis pilularis* DC. has come to dominance following removal of grazing. *B. pilularis* occurs on the *C. valida* study site and could easily overgrow much of the colony in a few years without grazing. We conclude, therefore, that *C. valida* is probably not threatened, but favored, by the existing grazing regime and that reductions in grazing should only be undertaken with extreme caution.

—LIAM H. DAVIS and ROBERT J. SHERMAN.

ANNOUNCEMENT

THE RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Mr. David Clarke, of the University of Illinois, Urbana is the recipient of the 1992 Rupert Barneby Award. Mr. Clarke will use the award to complete a taxonomic treatment of *Acacia* series *Gummiferae* of the Caribbean, both as part of his graduate thesis and as a contribution to the Flora of the Greater Antilles.

The New York Botanical Garden also invites applications for the 1993 Rupert Barneby Award. The award of $1,000.00 is to assist researchers planning to come to the New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a letter describing the project for which the award is sought, and how the collection at NYBG will benefit their research. Travel to NYBG should be planned between January 1, 1994 and January 31, 1995. The letter should be addressed to Dr. Enrique Forero, Director, Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126, USA, and received no later than December 3, 1993. Announcement of the recipient will be made by December 17. Anyone interested in making a contribution to THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Forero.

PRESIDENT'S REPORT

The past year has been both a challenging and an exciting time to be President ("La Presidente") of the California Botanical Society.

One challenge was locating a replacement for outgoing Editor Jon Keeley, who declined the opportunity to extend his editorship for another three years as a result of other demands on his time (including the next generation of Keeleys; congratulations!). Jon's exemplary performance will be a hard act to follow, so the Council was delighted when Bob Patterson accepted the rewarding challenge of editing MADROÑO. Bob will be learning the tricks of the trade from Jon on this issue, I understand.

As a major break from tradition, the annual banquet was held in southern California, hosted by the Santa Barbara Botanic Garden. This was one of the fruits of on-going discussions by the Council to make the Society a truly state-wide organization, not just the "Berkeley tea-club" as I once heard a disgruntled member refer to it. Bob Thorne was wonderfully appropriate as banquet speaker, in that the Society archives contain a rather scathing letter he wrote many years ago (which I was, alas, unable to locate) complaining about the lack of opportunities for participation in the Society by southern California botanists. We were therefore surprised by the disproportionately low representation from southern California; guess we northerners will have to issue a challenge the next time the banquet heads south!

Steve Junak, as Second Vice-President of the California Botanical Society (normally an office without duties, but not this year!), did a phenomenal job arranging a full two days of tours and a field trip to Santa Catalina island in addition to the evening banquet. Steve, Ed Schneider (Director of SBBG), and the staff of the Santa Barbara Botanic Garden are to be commended and much thanked for their efforts. They created a hard act to follow, but I believe that June McCaskill, Grady Webster, and the rest of the crew at UC–Davis will give them a run for their money when the banquet is held there next year in conjunction with the Graduate Student Meetings (to be organized by Webster's student Brian Smith).

Another break from the Society's recent history was a return to some of the activism of earlier decades. This was largely triggered by AB 1903, a state bill passed in 1991 that effectively established the Board of Forestry as the biological regulatory authority in California. As one result, all biological consultants would either have to become Registered Professional Foresters (the generalist position) or become certified in each specialty of relevance (e.g., botany, ecology, wetland delineation) by 31 December 1993. Although some form of botanical certification may be inevitable, the Council felt strongly that AB 1903 was totally inappropriate and therefore sent a letter supporting SB 1094, which would reduce the authority of the Board of Forestry to a more appropriate level. The selection of Peggy Fielder, who has a long-standing interest in conservation issues, as next year's President was influenced by the belief that this and similar issues will remain important.

Progress was made by various council members on numerous other projects. First Vice President Roxanne Bittman, in addition to arranging an excellent slate of speakers based on a biogeographical theme, drafted an article encouraging membership in the California Botanical Society that was published in a recent issue of the California Native Plant Society Bulletin. Council Member Chuck Quibell prepared a letter along similar lines to be distributed to academic colleagues and institutions. Recording Secretary Niall McCarten worked on a resolution regarding qualifications of botanists doing field studies. Treasurer Holly Forbes and Corresponding Secretary Margriet Wetherwax notified unpaid members of their status, a massive and long overdue undertaking. We hope that next year will see the fulfillment of several other long-term projects, notably the membership directory and "fire sale" of back issues of

MADROÑO. Because of current abysmally low interest rates, the Council decided to wait several years before making awards from the Carter fund, established in memory of Annetta Carter to promote research in Baja California.

I wish to thank the above-named and all other Council Members (Elizabeth Neese, Mike Vasey, Financial Officer Barry Anderson, Past President Jim Shevock) for making my year as President both successful and enjoyable. I welcome the new officers and wish them a productive year: Peggy Fiedler (President), Dennis Desjardin (1st Vice President), June McCaskill (2nd Vice President), Roxanne Bittman (Recording Secretary), and new Council Members Brent Mishler and John Little. I also again commend outgoing Editor Jon Keeley for a superb job, and recognize Cherie Wetzel's tremendous contribution in doing our taxes yet again. I also thank all the members who participated in this year's events and encourage the rest of you to get involved next year!

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY
JOINT PROCEEDINGS

Graduate Student Meeting and Annual Banquet
February 19, 1994

Once again the Graduate Student Meeting and the Annual Banquet will be held on the same day, this year on Saturday, February 19, 1994, on the campus of the University of California at Davis. The graduate student meeting will focus on the presentations of finished research, research in progress, or research proposals by graduate students in all plant-related fields. Further details will follow concerning the Graduate student Meeting. The Annual Banquet will be held at the Buehler Alumni Center and will feature a keynote address by Dr. Leslie D. Gottlieb of the Evolution and Ecology Section of the Division of Biology at U.C. Davis. The title of his talk will be "How do *Clarkias* make different flowers?"

For further information, write either June McCaskill (banquet info.) or Brian Smith (graduate info.) at the Section of Plant Biology, Robbins Hall, University of California, Davis, CA 95616-8537 or leave a message at (916) 752-0617.

Editor's Report for Volume 40

This annual report provides an opportunity for the editor to communicate the status of manuscripts received for publication in *Madrono* and to comment on the journal. Between 1 July 1992 and 30 June 1993, 55 manuscripts were received. These comprised 28 articles (10 published, 5 in press, 9 in review or revision and 4 rejected), 7 notes and 20 noteworthy collections. Volume 39 was composed of 24 articles (13 systematic and 11 ecological), 9 notes, numerous noteworthy collections, 5 book reviews, 2 obituaries, points of view commentary and many announcements.

The following persons deserve special recognition and thanks: those members of the Board of Editors that assisted me with reviews, Steven Timbrook for his continuing contribution of the annual Index and Table of Contents, James Ehleringer, Hal Mooney, Nona Chiariello, Susan D'Alcamo, and Phil Rundel for solicited contributions, Peter Raven for supporting our application for inclusion in Current Contents, and John Strother for his continued assistance with taxonomic details. A special note of appreciation goes to the list of reviewers of manuscripts. The Society owes them a special thanks for their thorough, tactful and helpful assistance. As I have said before, although high levels of community service normally set the research sciences apart from other professions, the reviewers I have dealt with this year have been very generous in their time. Also I thank Paul Zedler, Geoff Levin, Robert Ornduff, Jonathan Comstock and Melanie Baer-Keeley for writing book reviews.

This issue marks the end of my tenure as editor. I thank the California Botanical Society for the opportunity to serve this very important organization and look forward to further opportunities to serve. One of the important challenges yet to be addressed by the Society is how to include fuller participation by the membership as society officers. A major limitation to participation by members outside of the Bay Area is the difficulty in attending monthly business meetings. I suggest that either monthly meetings need to rotate around the State or funds be obtained to pay for transportation to officers from other regions.

I here offer a special thanks to Robert Patterson for his enthusiasm in taking on the editorship for the next three years.—Jon E. Keeley.

A Tribute to James C. Hickman
(20 April 1941–15 June 1993)

A long standing member of the California Botanical Society and former editor of Madrono passed away this year. While a formal obituary is planned for a future issue, we here present a personal tribute.

Jim Hickman, editor of the new Jepson Manual, died recently of Aids-related pneumonia. The new field guide is the result of Jim's planning and organization. With a dedicated group of authors, artists, editors, and volunteers, over 200 people in all, and the support of the Friends of the Jepson Herbarium, the manual was completed on time and with distinction. We are grateful that Jim lived long enough to see the result of his efforts.

During the late 70's and early 80's, Jim and Larry Heckard, of the Jepson Herbarium, were collaborating on the flora of Snow Mountain, a peak of the Inner North Coast Ranges. The need to revise and update existing state field guides became very evident as they worked on the project—the rest is history—as they say.

The publication of *The Jepson Manual: Higher Plants of California* is a direct result of that collaboration. When he started in 1982, Jim was to do a revision of the original 1925 Jepson *Manual of Flowering Plants,* working on a 10-year schedule. As the project progressed, the scope and form evolved to reflect the complexities and changes of the last 50 years of botanical research. The new manual is not only up-to-date, but "is based on a virtually revolutionary premise: a single work of this magnitude can be simultaneously accessible to dedicated beginners and indispensable to professional botanists."

Though it seems like a much longer time, I first met Jim in 1979. As with so many of his fans, our meeting was in a classroom—he on the "up" side of the podium. As a returning student, the spring course on the California flora and plant communities was one of the first classes I wanted to take, and, as it turned out, it was the first he had taught at Berkeley. It was a wonderful introduction to botany at Cal. Jim was not only enthusiastic and knowledgeable about botany and ecology in general, and the California flora especially, but a truly inspired and inspiring teacher.

Since that time, many of his students and colleagues have confirmed my impression. Jim will be remembered particularly as a teacher. He was anxious to communicate his love of the plant world, and nature in general, to youthful students, and to the mature laity, where amateur and professional merge in a powerful force for heightened appreciation and dedicated conservation.

Besides teaching at Washington State University, Pullman, Swarthmore College, and University of California, Berkeley, Jim was Associate Program Director for Systematic Biology (1975–1976) with the National Science Foundation. He became a Shanti volunteer in 1983 and was active with other Aids-related groups.

Jim taught at Swarthmore for eight years after teaching at Pullman and before coming to Berkeley. Many of his former students continued to seek him out as they went into the world. Whether they were looking for a job, applying to graduate school, or needed direction in their studies or their lives, they came—asking advice, seeking support, looking to a friend. And a friend he was!

I started working with Jim and Larry in 1983—first as a volunteer and then as a staff member. Jim was the ideal boss and we became good friends. He was as enthusiastic and generous about sharing his many outside interests as he was in sharing his love of natural history. I am very grateful for all that I learned from him and honored to have been a part of his life.

Jim's life was a celebration. Music, intellectual curiosity, and friends were his touchstones. His passing reflected his life—one of awareness, courage, and surrounded

by friends. James C. Hickman's name on *The Jepson Manual* is a fitting memorial to his vision and perseverance.

—SUSAN D'ALCAMO

I knew Jim Hickman throughout his tragically brief career, first while he was a graduate student at the University of Oregon, then as a Professor at Swarthmore, and finally during his period at the University of California at Berkeley. He had a very important influence on my own career. A number of the absolutely first rate undergraduate students that he attracted to biology at Swarthmore subsequently pursued graduate studies at Stanford, much to our benefit. Subsequently these students have attained leading roles in teaching and research in population biology. During the period between Swarthmore and in assuming his duties with the Jepson Herbarium Jim collaborated with Nona Chiariello and myself on an ecological study of the annual grasslands on Jasper Ridge at Stanford. I felt that this was an important study but it had the unfortunate result of convincing Jim that plant systematics would be more rewarding than counting seedlings of very small plants of different species that had convergent morphologies at an early stage. Ecology's loss was certainly plant systematic's gain as his magnificent new flora has subsequently shown. Now both ecology and plant systematics have lost his unusual talents and I have lost a good friend.

—H. A. MOONEY

During his years of teaching at Swarthmore College (1970–1978), Jim Hickman had a profound influence on the generation of students who studied plant taxonomy and plant ecology with him. He was universally respected as a rigorous and intellectually challenging teacher, and loved for his ability to nurture potential and bring out the best in everyone. Influenced by Jim's teaching, dozens of the undergraduates from his classes at Swarthmore continued in areas related to ecology or taxonomy.

As a teacher, Jim set extremely high standards but had the gift of making them reachable. Often even the best students became terribly lost early in Jim's systematics class when they were handed a mammoth, mimeographed syllabus of plant families and took their first plunge into the Magnoliidae. Jim had included in the syllabus a wealth of details about numerous genera, and even species, in each family of flowering plants. After one exam that devastated much of the class, one student complained of the difficulty of knowing what was important for the exam. Jim replied that everything was important, but then added with characteristic humor and compassion, that the key was in finding out what was sufficient. Eventually we understood that Jim had provided multiple routes to learning plant families. On Sunday afternoons, plant specimens from the week's taxonomy lab drew students in to the lab to review, compare notes, commiserate, and become friends. Many of us retained more from that class than any other in college. His syllabus has since been duplicated many times and passed on to many more students than Jim personally taught. It served as an important foundation for those of us who went on to teach similar courses.

Jim's plant ecology class and honors seminar were equally challenging and inspiring. He forced us to think critically and independently. Years before the publication of John Harper's Population Biology of Plants, Jim introduced ideas and perspectives from the emerging field of plant population biology into his teaching. The course was also an intense introduction to the trials and joys of field ecology. The plant ecology field trip to the Pine Barrens was legendary. After a manic weekend braving poison ivy, Smilax, weather, and our own camp cooking to run transects in a variety of habitats, we emerged with an appreciation for the mechanisms structuring Pine Barrens communities. That trip was also an introduction to the rewards and stresses of collaborative data collection and analysis. The cooperative approach to science that Jim successfully encouraged helped to shape lifetime attitudes for many of us.

Important as his academic orientation was, Jim's greater gift to his students was in recognizing something special, and different, in each of them. Those of us who were most overwhelmed by academic or other college pressures were most aware of this. He supported us when we were struggling and credited us when we mastered concepts, as though both were integral parts of learning. He recognized our abilities whenever he could. We remember one crucial seminar when Jim declared that a student's experimental design was superior to his own, and he asked her to explain it to the class.

Jim's outlook influenced and spread through his classes, and it fostered friendships that are among our most important. Later, Jim gracefully, and gladly, stepped out of the role of mentor and became a colleague, collaborator, and friend, an adjustment that seemed minor because of the respect he showed his students.

As our teacher, Jim passed on to us the finest example of scientific scholarship coupled with a patient and caring focus on the student as a person. He is the teacher and scholar we use as a yardstick in our lives and our careers.

—Nona Chiariello
—Johanna Schmitt
—Elizabeth L. Taylor
—Virginia Boucher

Reviewers for Volume 40

Kelly Allred
Gregory Anderson
Bruce Baldwin
Bruce Bartholomew
Randall Bayer
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INDEX TO VOLUME 40

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

Geum urbanum, noteworthy collection from OR, 182.

Glacier National Park, MT, additions to flora, 126.

Gramineae (see Poaceae).

Grazing (see *Chorizanthe*).

Growth rings, utility in age determination of chaparral shrubs, 1.

Halimolobos perplexa, noteworthy collection from MT, 271.

Haplopappus aberrans, noteworthy collection from MT, 272.

Helianthella californica var. *nevadensis,* noteworthy collection from CA, 133.

Helianthus paradoxus, noteworthy collection from NM, 274.

Herbivores and understory plants, effects of timber harvest treatments on in NE CA, 31.

Hexalectris warnockii, noteworthy collection from AZ, 132.

Hydrophyllaceae (see *Phacelia*).

Hymenoxys jamesii, new species from AZ, 43.

Idaho: Noteworthy collections: *Asclepias incarnata,* 135; *Bryonia alba,* 180; *Chaenorrhinum minus,* 136; *Euphorbia dentata,* 135; *Galium pedemontanum,* 179; *Verbascum virgatum,* 135.

Juncaceae (see *Juncus*).

Juncus triglumis var. *albescens,* noteworthy collection from OR, 183.

Juniperus virginiana, noteworthy collection from OR, 183.

Klamath Mountains, CA (see *Asarum*).

Kobresia bellardii, noteworthy collection from CA, 66.

Labiatae (see Lamiaceae).

Lamiaceae: Noteworthy collections: *Monardella douglasii* var. *venosa* from AZ, 269; *Salvia davidsonii* from NM, 137; *Teucrium glandulosum* from AZ, 178.

Lava Beds National Monument, CA, ferns of, 174.

Leguminosae (see Fabaceae).

Lepidium heterophyllum, noteworthy collection from OR, 184.

Liliaceae (see *Lilium*).

Lilium parryi, noteworthy collection from Mexico, 270.

Limnanthaceae (see *Limnanthes*).

Limnanthes alba, noteworthy collection from OR, 183.

Liparis loeselii, noteworthy collection from MT, 272.

Lycopodiaceae (see *Lycopodium*).

Lycopodium inundatum, noteworthy collection from MT, 271.

Malacothrix phaeocarpa, new species from CA, 101.

Malvaceae (see *Abutilon*).

Mexico: Additions to the flora of the Sierra de la Laguna, Baja California, 15. Noteworthy collections: *Lilium parryi,* and *Rumex orthoneurus,* 270.

Mirabilis tenuiloba, noteworthy collection from AZ, 178.

Monardella douglasii var. *venosa,* noteworthy collection from AZ, 269.

Montana: Glacier National Park, additions to flora, 126; pollinator exclusion and loss of fitness in *Silene spaldingii,* 193.

Noteworthy collections: *Halimolobos perplexa, Haplopappus aberrans, Liparis loeselii, Lycopodium inundatum,* 271.

Muhlenbergia argentea and *M. lucida,* allozyme differentiation, 148.

Neotoma: plant remains from Holocene packrat middens in AZ, 246.

Nevada: *Antennaria soliceps,* isozyme variation, ecology and phytogeography in alpine Spring Mountains, 75.

New Mexico: Noteworthy collections: *Cryptantha gracilis, C. recurvata, Epipactis helleborine, Helianthus paradoxus, Oxytropis deflexa* var. *deflexa,* 273; *Panicum mohavense,* 136; *Phacelia cephalotes, Plantago elongata* subsp. *elongata,* 274; *Salvia davidsonii,* 136.

Nickel, hyperaccumulation in *Arenaria rubella,* 25.

Nyctaginaceae (see *Mirabilis*).

Onagraceae (see *Clarkia*).

Orchidaceae: Noteworthy collections: *Cephalanthera austinae* from CA, 133; *Epipactis helleborine* from NM, 274; *Hexalectris warnockii* from AZ, 132;

Turdus migratorius, dispersal of *Crataegus* seeds by, 108.

Umbelliferae (see Apiaceae).
Understory plants and herbivores in ne CA, effects of timber harvest treatments on, 31.
Utah (see *Atriplex*).

Valerianaceae (see *Centranthus*).
Verbascum virgatum, noteworthy collection from ID, 135.
Viola langsdorfii, noteworthy collection from CA, 135.
Violaceae (see *Viola*).

Viguiera multiflora var. *macrocephela,* noteworthy collection from AZ, 132.

Washington: *Amorpha fruticosa,* invasion of along Columbia and Snake rivers in OR and WA, 62; *Arenaria rubella,* hyperaccumulation of nickel, 25.
New taxon: **Silene douglasii** var. **rupinae,** 96.
Noteworthy collections: *Abutilon theophrasti,* 184; *Anthriscus sylvestris,* 185; *Chaenorrhinum minus,* 136; *Platanthera chorisiana,* 66; *P. orbiculata* var. *orbiculata,* 138.

ANNOUNCEMENT

New Publications

Effects of Resource Distribution on Animal-Plant Interactions. Edited by M. D. Hunter, T. Ohgushi, and P. W. Price. 1992. Academic Press, San Diego, CA. xi + 505 p. Hardcover, $95.00. ISBN 0-12-361955-6. Fourteen chapters contributed by plant and animal specialists.

The Ecology of Regeneration in Plant Communities. Edited by Michael Fenner. 1992. C.A.B. International, Wallingford, Oxon, U.K. x + 373 p. Hardcover, $94.00. ISBN 0-85198-726-5. Contributions by 17 authors cover seed dispersal, seed banks, seed dormancy/germination and establishment.

The Unity of Evolutionary Biology. Edited by Elizabeth C. Dudley. 1991. Dioscorides Press, Portland, OR. Two-volume set. 1048 p. Hardcover, $125.00. ISBN 0-931146-19-4. Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology. A diverse collection of papers on genetics, ecology, systematics and evolution.

The Grass Genera of the World. By Leslie Watson and Michael J. Dallwitz. 1992. 1038 p. Hardcover, $142.50. ISBN 0-85198-802-4. C.A.B. International, Wallingford, Oxon, U.K. Detailed data base on grass genera of the world.

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Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used in Madroño 39(2). 1992. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum,* 7th ed. Names of authors of scientific names should be abbreviated according to the Kew *Draft Index of Author Abbreviations* (1980) and, if not included in this index, spelled out in full. Titles of all periodicals, serials, and books should be given in full. Books should include the place and date of publication, publisher, and edition, if other than the first.

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CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME XXXXI
1994

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DEDICATION

James R. Griffin, through a lifetime of patient, meticulous study, has accumulated and shared a wealth of information about California's plants. He worked first on *Pinus,* as a graduate student at Berkeley, where he received his M.S. in Forestry in 1957 and his Ph.D. in Botany in 1962, and then when he was a Research Forester for the Pacific Southwest Forest & Range Experiment Station in Redding. His book, The Distribution of Forest Trees in California, co-authored with W. B. Critchfield in 1972, is a classic and useful work. Jim joined the staff at Hastings Natural History Reservation of the Museum of Vertebrate Zoology at U.C. Berkeley in 1967. His landmark studies on oaks, their ecology and regeneration, are probably the best-known works of his twenty-five year career at Hastings. Trees have not been Jim's only interest however. Anyone who has taken a field trip with him will know how intimately he knows every ridge and valley and most populations of plants at Hastings and in the entire Monterey and San Benito area. In fact, he has gathered data over two decades on 25 grassland plots on old fields at Hastings, the second such study ever to be done in California. In these plots he has studied the progress of every seedling of every species through each year. Perhaps because he himself finds the plants and their environment so interesting, he has a remarkable ability to bring them alive and make them interesting to others. His droll sense of humor and unique turn of phrase add to this, and he has the same knack for characterizing people, historical and current. Not surprisingly, he has always been in demand as a field trip leader and as an author of popular articles, and he has been effective in working with local

residents on conservation issues. Jim has been a mentor and friend to many of the biologists who have done their graduate or postgraduate studies at Hastings, and to others who have passed through Hastings for one reason or another or who have sought him out deliberately. By listening with genuine interest and an open mind, he has encouraged and given heart to many aspiring taxonomists and ecologists. Like the oaks and pines, he has made an enduring and endearing contribution to California botany, and it is in appreciation of this and with great pleasure that we dedicate this volume of Madroño to James R. Griffin.

TABLE OF CONTENTS

Dates of Publication of Madroño, Volume 41

83
PT

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

∞ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**

ARCTOSTAPHYLOS RAINBOWENSIS, A NEW BURL-FORMING MANZANITA FROM NORTHERN SAN DIEGO COUNTY, CALIFORNIA

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Abstract

Arctostaphylos rainbowensis Keeley & Massihi is a new burl-forming manzanita restricted to northwestern San Diego County and adjacent Riverside County. Previously it had been treated as a disjunct population of the largely Baja Californian *A. peninsularis* P. Wells or a hybrid between *A. glandulosa* Eastw. and *A. glauca* Lindley. Principal components analysis on 48 characters shows that *A. rainbowensis* is distinct from all three of these species. It differs from *A. peninsularis* in its larger leaves with almost twice as many stomata on the abaxial as on the adaxial surface, sparsely glandular puberulent branchlets and rachises, more widely spaced floral bracts, shorter and thicker pedicels, larger fruits that are darker and purple tinged, mealy mesocarp and smooth endocarp. *Arctostaphylos rainbowensis* differs further from *A. peninsularis* in its ecological distribution; *A. peninsularis* is a species of the interior, distributed at elevations above 1200 m whereas *A. rainbowensis* is a low elevation coastal range species. *Arctostaphylos rainbowensis* is distinct from *A. glandulosa* in its diploid chromosome number, non-scabrous leaves, reduced floral bracts, and larger fruits that are round with a solid stone. It differs from *A. glauca* in having a burl, non-reflexed floral bracts, and smaller, non-viscid fruits. *Arctostaphylos rainbowensis* is restricted to approximately 275 km² in a region that is undergoing rapid development. In the last 20 years many of the populations have been extirpated, and the species needs legal protection.

Resumen

Arctostaphylos rainbowensis Keeley & Massihi, es una especie nueva de "manzanita" que desarrolla nudos, y que está distribuída desde el noroeste del Condado de San Diego hasta los límites del Condado de Riverside, en California. Esta especie ha sido referida como una población disjunta de *A. peninsularis* que ocurre en Baja California, o como un híbrido entre *A. glandulosa* y *A. glauca.* Un análisis componentes principio de 48 carácteres, revelaron que *Arctostaphylos rainbowensis* es distinta a los tres taxa anteriores. Lo se diferencia de *A. peninsularis* porque sus hojas son más grandes, el número de estomas en la superficie abaxial es casi el doble que en la adaxial, raquis y ramificaciones pulverulento-glanduloso, brácteas florales más cortas y separadas, con frutos más grandes y de color púrpura oscuro. Además, *Arctostaphylos rainbowensis* se distingue de *A. peninsularis* en su distribución ecológica, ya que *A. peninsularis* es una especie que se distribuye en montañas por arriba de 1200 m, mientras que *A. rainbowensis* es típica de bajas elevaciones cercanas a la costa. Se distingue de *A. glandulosa* en que es diploide, con un número cromosómico de 13; presenta además hojas no escabrosas, brácteas florales reducidas y frutos grandes, globosos y duros (sólidos). *Arctostaphylos rainbowensis* es separable de *A. glauca* por la presencia de nudos, brácteas florales no reflexas y frutos pequeños, glabros y no viscidos. *Arctostaphylos rainbowensis* esta restringido a una región de aproximadamente 275 km² en una región sometida a un rapido desarrollo urbano. Se estima que en el futuro en un periódo de 20 años, una fracción de estas poblaciones serán eliminadas, por lo que estas especies tendrán que tener una protección legal.

In 1973 a species of *Arctostaphylos* (Ericaceae) new to the California flora was collected by the first author from northern San Diego County. A manuscript naming this new taxon was rejected because one reviewer claimed it was merely a disjunct population of the newly described *A. peninsularis* P. Wells from interior ranges of Baja California (Wells 1972). Subsequently, the San Diego taxon was reported as a range extension of the Baja Californian *A. peninsularis* (Keeley 1974) and others have since listed it in local floras (Beauchamp 1986) and rare plant inventories (Smith and Berg 1988). In the new *Jepson Manual,* however, Wells (1993) omitted it because he no longer believes it is *A. peninsularis,* but now considers it an errant hybrid between *A. glauca* Lindley and *A. glandulosa* Eastw. (Wells personal communication and annotated specimens SD 118009, 118010).

Phenetic analysis reported here demonstrates that the San Diego County taxon is distinct from *A. peninsularis* and is not a hybrid population. This manzanita is described as a new species.

Species Treatment

Arctostaphylos rainbowensis J. Keeley & Massihi, sp. nov. (Fig. 1).—
Type: USA, California, San Diego Co., off Rainbow Crest Rd., NE of Rainbow, 3 Aug 1973, *J. E. Keeley 3548* (holotype, LOC; isotypes, CAS, RSA, SD).

Frutices erecti aut arborescentes, 1–4 m alti; caudex tumescens, repullulans post combustum; cortex levis ruber; ramuli glabrati, sparse glandulo-puberuli; folia glauca vel sparse glauca, stomatifera infra duplicato supra, elliptico-ovata, basi rotundatus; petiolo 6–12 mm longo; inflorescentia nascens descendens, paniculata, ramulis 4–10, glabratis, sparse glandulo-puberulis; bracteae subulatae, acuminatae, glabratae, 2–4 mm longae; pedicelli glabri, 3–5 mm longi; corolla alba, urceolata, 6–8 mm longa, 6 mm lata; ovarium glabrum; drupa globosa, glabra, glauca, purpurata, 8–12 mm diametro, mesocarpio crasso, endocarpio solido, nuculis coalescentibus.

Erect shrub or arborescent, 1–4 m high, with large globose burl formed early in development (evident on plants a year old) or large and platform-like on resprouted shrubs. Bark red-brown, smooth. Branchlets seemingly glabrous but microscopically sparsely glandular-puberulent. Leaves seemingly isofacial but with nearly twice as many stomata on lower (abaxial) surface; petioles 6–12 mm; blades 35–50 mm long, 20–35 mm wide, elliptic-ovate, glabrous, moderately glaucous to only slightly glaucous, the margin occasionally serrate, especially on recent resprouts, the base rounded. Panicle descending when immature with well-spaced non-overlapping bracts and exposed buds, 4–10 branches; bracts 2–4 mm, deltoid-subulate,
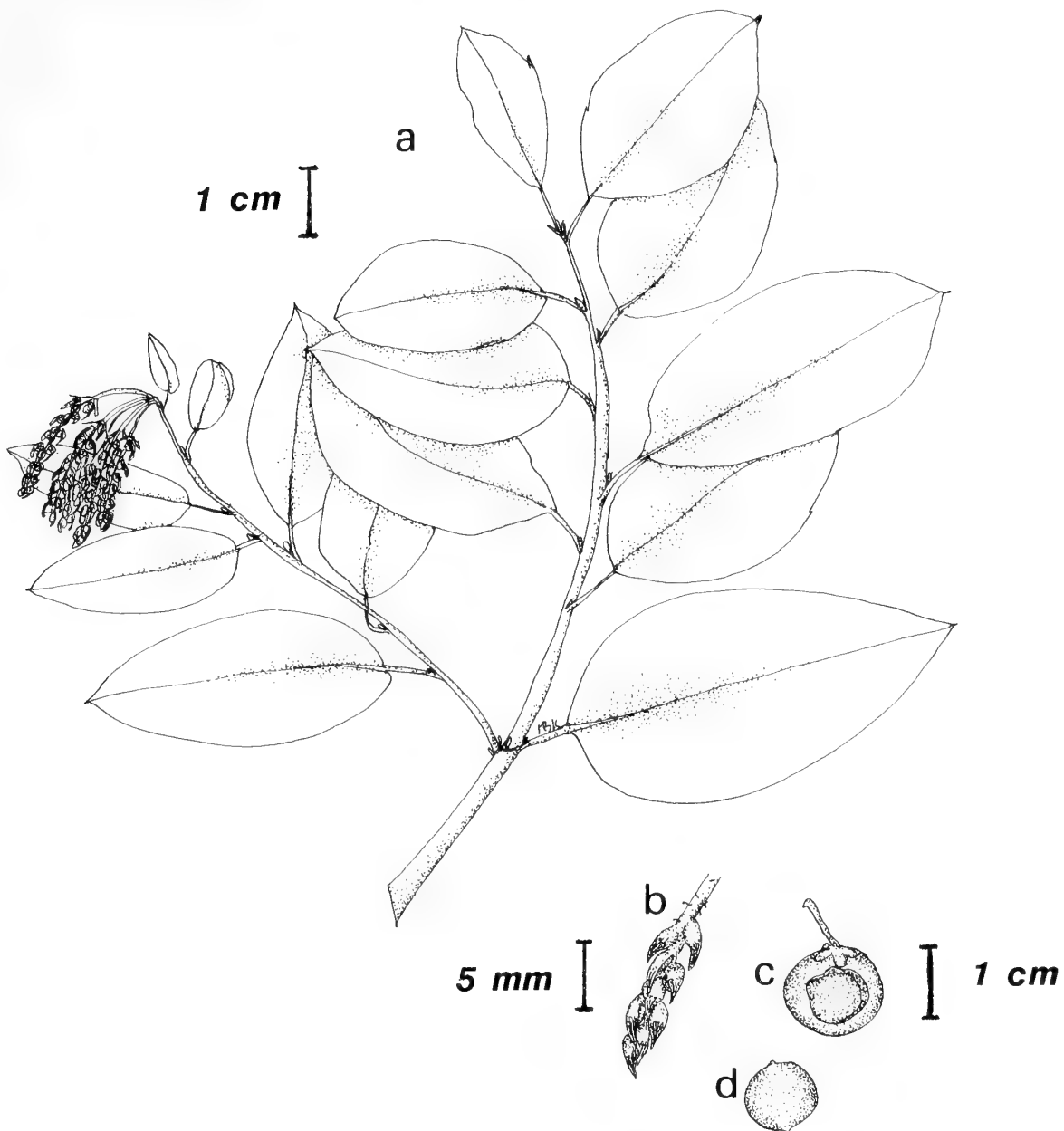
FIG. 1. *Arctostaphylos rainbowensis* (*J. Keeley 3548*). a. Branchlet with nascent inflorescence. b. Single branch of nascent inflorescence. c. Fruit, sepals, and pedicel; mesocarp and endocarp exposed. d. Stone endocarp enclosing multiple seeds (drawing by Melanie Baer Keeley).

keeled, upper-half early marcescent; rachis seemingly glabrous but sparsely covered with short glandular hairs; panicle compact in flower but widely spreading in fruit. Corolla white, urceolate, 5-lobed, pubescent inside, 6–8 mm long; inflated filament bases densely hairy; ovary glabrous. Fruiting pedicel glabrous, thick, 3–5 mm long. Sepals weakly appressed to fruit. Mature fruit globose, 8–12 mm, dark brown with distinct purple tinge and often with whitish bloom, glabrous; mesocarp moderately mealy, dark tan; stone solid, apiculate, without ridges, weakly sculptured. Flowering January–February. $n = 13$ (J. Keeley). The epithet is for the community of Rainbow, near the center of distribution for this species.

Distribution and habit. Arctostaphylos rainbowensis is restricted to northern San Diego County, north of the San Luis Rey River, and southern Riverside County, south of Pauba Valley (Fig. 2), between 300–600 m. It is well represented around the community of Rainbow and east to Mt. Olympus. Its eastern boundary is the Aqua Tibia range and its western boundary is the Santa Margarita Mountains. Total area is approximately 275 km^2. The coastal ranges around Rainbow are dominated by exposed bedrock and very large boulders of acid igneous rock (USDA 1973). Although such sites have been described as of no agricultural value (USDA 1973), in the past two decades many *A. rainbowensis* sites have been replaced by avocado orchards.

Throughout its range *A. rainbowensis* is apparently the sole *Arctostaphylos* species. However, on the edges of its range, in the eastern Santa Margarita Mountains and the western Agua Tibia Mountains, it is sympatric with *A. glandulosa*. These populations usually include individuals that combine traits of both species, suggesting hybridization and introgression between them. *Arctostaphylos glauca* grows in the interior east of *A. rainbowensis*. *Arctostaphylos peninsularis* is restricted to the interior ranges of northern Baja California and the desert slopes of interior ranges of San Diego and possibly Riverside counties above 1200 m (Keeley unpublished data).

Arctostaphylos rainbowensis is a vigorously resprouting shrub that also produces copious fruits and readily establishes seedlings on disturbed sites created either by wildfires or, more commonly, by bulldozers. On the eastern edge of its range, flowers and fruits are often heavily infested with boring insects.

PARATYPES: USA, California, San Diego Co., Recent burn along unnamed dirt road 6 km N of S–13 off De Luz Rd, 250 m, 29 July 1973, *J. Keeley 3411* (LOC); W face of Mt. Olympus, E of Rainbow, 500 m, 18 Sept 1992, *J. Keeley 21225* (LOC); Pala Rd, 1.5 km S of Rancho Hts Rd, 410 m, 10 Aug 1992, *A. Massihi, R. Goar, J. Keeley 19333* (LOC); Rainbow Hts. Rd, 100 m west of Via Ladera, Rainbow, 400 m, 17 Jan 1993, *Jon E. Keeley 22559* (LOC). Riverside Co., amongst boulders, W of Temecula, 1 km S of Carancho Rd, and W of De Luz Rd, 600 m, 11 Aug 1992, *A. Massihi, R. Goar, J. Keeley 19489* (LOC).

KEY TO THE SOUTHERN CALIFORNIA BURL-FORMING
ARCTOSTAPHYLOS

The following key, based on studies still in progress, will assist in separating *Arctostaphylos rainbowensis* from other burl-forming manzanitas in southern California. It includes three other taxa not treated in the new *Jepson Manual* (Wells 1993):
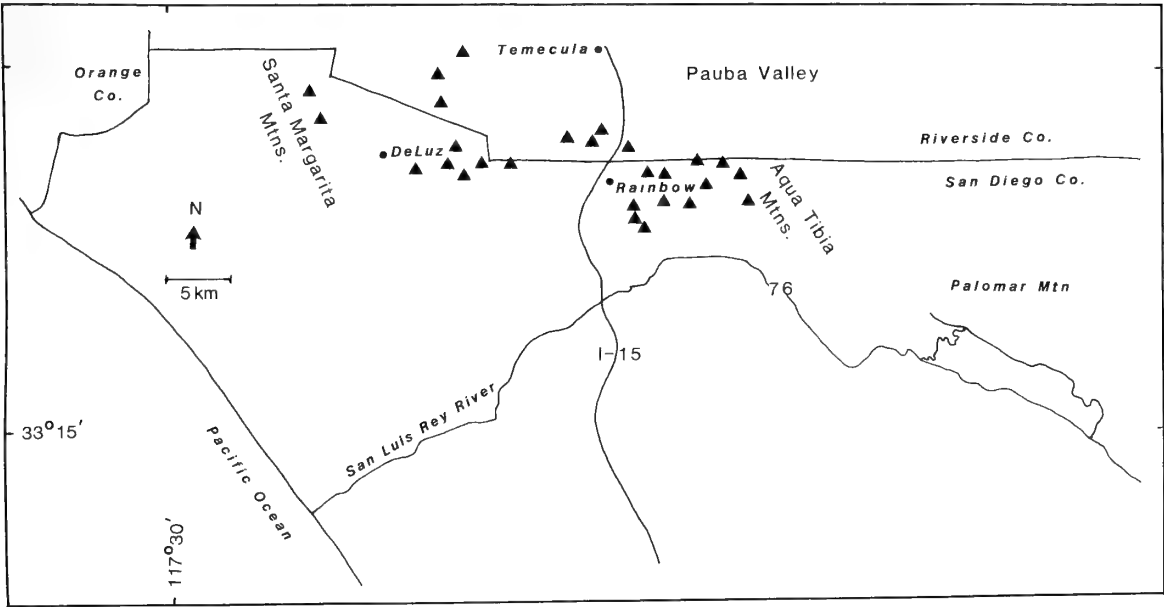
FIG. 2.   Distribution of *Arctostaphylos rainbowensis*. Known localities are indicated by triangles.

1. Fruits flattened perpendicular to pedicel (width 1.5–1.7× > length); mesocarp thick and mealy; endocarp separable into 3–5 pyrenes; foliaceous bracts subtending inflorescence 5–15 mm; panicle few branched, compact; (other characters variable); widespread .... *A. glandulosa*
1'. Fruits globose (width = length); mesocarp thinner, papery, leathery or mealy; endocarp a solid stone; lower bracts highly reduced or absent; panicle few–many branched, spreading
    2. Branchlets and rachises tomentose to puberulent; mesocarp leathery
        3. Leaves green, not glaucous; fruits 10–12 mm; montane ....
            .... *A. parryana* Lemmon
            (although *A. parryana* is non-burl forming throughout most of its range, there is an undescribed burl-forming *A. parryana* above 1400 m in the San Bernardino and San Gabriel Mtns; it apparently hybridizes with *A. glandulosa* in the latter range and, pending further study, *A. gabrielensis* P. Wells is here treated as such a hybrid).
        3'. Leaves glaucous; fruits smaller, 8–10 mm; desert slopes ..... (undescribed taxon with affinities to *A. parryana* and *A. peninsularis,* in the San Jacinto, Santa Rosa, Hot Springs and San Ysidro mtns)
    2'. Branchlets and rachises seemingly glabrous and mostly glaucous; mesocarp not leathery
        4. Inflorescence bracts not overlapping, tips marcescent; fruits purplish brown; mesocarp mealy; coastal range .... *A. rainbowensis*
        4'. Inflorescence bracts tightly overlapping, not marcescent; fruits orange-red; mesocarp papery; desert slopes .... *A. peninsularis* (uncommon, NW In-Ko-Pah Mtns, some populations appear to intergrade with *A. glandulosa*)

PHENETIC ANALYSIS OF *A. RAINBOWENSIS* AND OTHER *ARCTOSTAPHYLOS*

Morphometric data were collected from herbarium specimens and used to compare *A. rainbowensis* with the other three species dis-

TABLE 1. CHARACTERS USED IN PRINCIPAL COMPONENTS ANALYSIS AND FACTOR LOADINGS FOR ALL SPECIES (*A. RAINBOWENSIS*, *A. PENINSULARIS*, *A. GLAUCA*, *A. GLANDULOSA*) AND WITHOUT *A. GLANDULOSA*. Percentage of total variance explained was 37% for Factor 1 and 17% for Factor 2 with all four species and 27% for Factor 1 and 19% for Factor 2 with *A. glandulosa* removed.

Character	All four species (Fig. 3)		Without *A. glandulosa* (Fig. 4)	
	Factor 1	Factor 2	Factor 1	Factor 2
Burl	0.30	−0.86	0.89	−0.12
Leaf blade length	0.03	−0.75	0.75	0.26
Leaf blade width	−0.19	−0.45	0.46	0.35
Ratio leaf width/length	−0.28	0.30	−0.31	0.15
Basal angle	0.27	−0.58	0.59	−0.22
Apical angle	0.30	−0.37	0.36	−0.10
Blade shape	0.22	−0.29	0.26	−0.20
Petiole length	−0.25	−0.33	0.31	0.29
Leaf color	0.20	−0.22	0.27	0.28
Leaf glaucousness	0.55	−0.47	0.64	0.20
Leaf scabrousness	0.98	0.08	0.04	0.00
Density of abaxial stomata	0.15	0.43	0.48	0.36
Density of adaxial stomata	0.37	−0.37	−0.39	0.47
Abaxial stomata/adaxial stomata	0.16	−0.76	0.78	0.36
Branchlet pubescence	0.93	−0.26	0.92	0.05
Petiole pubescence	0.97	0.08	0.07	−0.01
Leaf blade pubescence	0.94	0.09	−0.03	0.12
Rachis pubescence	0.93	−0.28	0.92	0.09
Pedicel pubescence	0.82	0.32	−0.49	0.82
Branchlet glandularity	0.94	−0.26	0.94	0.06
Petiole glandularity	0.97	0.06	0.15	0.00
Leaf blade glandularity	0.78	0.06	−0.07	0.05
Rachis glandularity	0.93	−0.25	0.91	0.15
Pedicel glandularity	0.58	0.46	−0.50	0.82
Fruit glandularity	0.09	0.56	−0.52	0.82
Inflorescence length	−0.32	−0.34	0.32	0.09
Number of rachis branches	−0.21	−0.44	0.44	0.00
Bract spacing	−0.69	−0.15	0.17	0.80
Bract keel	−0.88	−0.30	0.64	0.58
Bract shape	−0.06	0.59	−0.12	0.06
Bract marcescence	−0.54	−0.75	0.89	−0.16
Bract reflexed	−0.16	0.44	−0.42	0.76
Bract tip hooked	−0.21	0.51	−0.60	−0.66
Bract length				
Subtending inflorescence	0.84	0.23	−0.32	0.03
Subtending flower bud	0.71	0.12	−0.07	0.58
Pedicel length	−0.05	0.58	−0.60	−0.15
Pedicel width	0.02	−0.74	0.79	0.04
Sepal reflexed	0.59	0.30	−0.34	−0.43
Fruit color	−0.49	0.65	0.74	0.35
Fruit length	−0.66	0.20	−0.28	0.73
Fruit width/fruit length	−0.50	0.31	0.14	−0.00
Fruit weight	−0.47	0.26	−0.25	0.87
Pericarp weight	−0.35	−0.02	−0.02	0.69
Endocarp weight	−0.47	0.33	−0.32	0.84
Mesocarp texture	−0.55	0.74	−0.92	0.16
Endocarp segments	0.91	0.05	0.14	0.01
Endocarp lateral ridges	0.66	0.27	−0.32	−0.70
Endocarp sculpturing	0.55	0.41	−0.49	−0.71

cussed in the introduction. A principal components analysis was plotted to illustrate the interrelationships among all specimens studied.

Species. We collected data from 160 specimens of *A. rainbowensis* from throughout its range (Fig. 2); 70 specimens of *A. peninsularis* from the Sierra San Pedro Mártir and Sierra Juárez of northern Baja California; 30 specimens of *A. glauca* from its range east of *A. rainbowensis* and 30 specimens of *A. glandulosa* from its range south and east of *A. rainbowensis.*

Methods. We used 48 characters in this study; 16 continuous quantitative, 2 meristic, and 27 qualitative characters were recorded and 3 were calculated ratios (Table 1). Qualitative characters were given a ranking from 1 to 5 and each specimen was scored twice by two different persons. For quantitative characters, two samples were measured or weighted for each specimen and the mean was used in the analysis. All character states were standardized by transforming each variable with a z-score obtained by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. This data matrix was used for ordination with principal components analysis using SYSTAT for Windows, Version 5 (Evanston, IL). Characters were compared between populations and species with the Kruskal-Wallis test.

Chromosome counts for *A. rainbowensis* were made from buds collected in January just as they were beginning to enlarge, and preserved in 3:1 ethanol: glacial acetic. Anthers, not yet pigmented, were selected under low power and squashed with aceto-carmine and viewed at $100\times$. This character was not utilized in the principal components analysis due to the lack of data for *A. peninsularis.*

Stomatal distribution was determined from epidermal peels made of clear nail polish and examined under $40\times$. All stomata in the field of view were counted and the mean of five different parts of the leaf was used in the analysis.

Results and discussion. The plot of the first two principal components from the analysis of all 290 individual specimens is shown in Figure 3. Ellipses enclose all points for a species and illustrate a clear separation of *Arctostaphylos rainbowensis* from the other three species. Also evident is the overlap in the distribution of *A. peninsularis* and *A. glauca* specimens; all specimens within the zone of overlap with *A. glauca* were the non-burl forming *A. peninsularis* subsp. *juarezensis* J. Keeley, Massihi & Goar.

The loadings of the variables on the first two components indicate the extent to which each character contributes to the variance in this plane (Table 1). Indumentum characters, lower bract length, bract keel and number of endocarp segments contributed most to
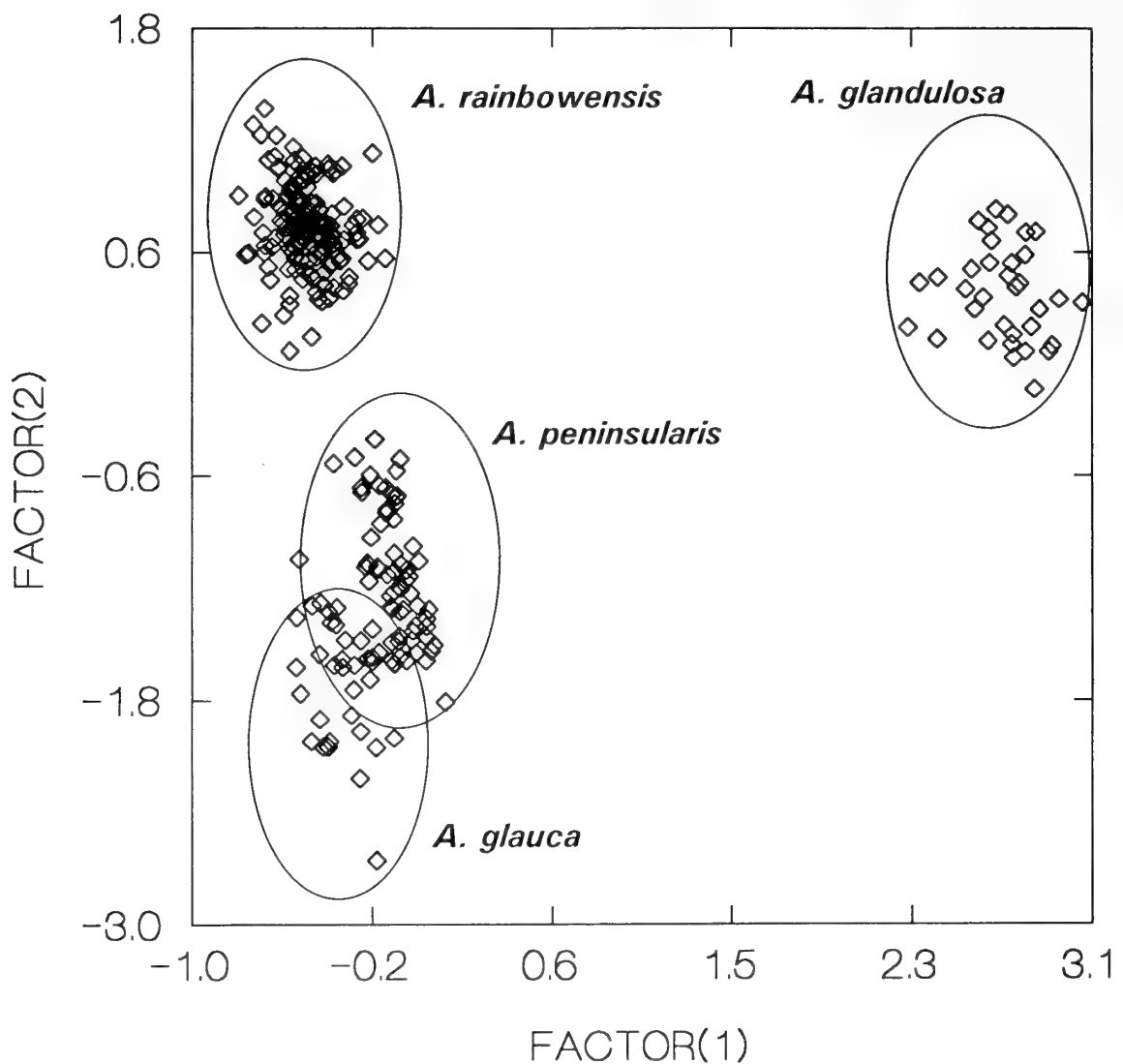
Fig. 3. Plot of principal component analysis using all four species. Relative position of 290 manzanita specimens on the first two principal components of the 48 character correlation matrix. See Table 1 for factor loadings. *Arctostaphylos rainbowensis*, n = 160; *A. peninsularis*, n = 70; *A. glauca*, n = 30; *A. glandulosa*, n = 30.

the separation of *A. glandulosa* from the other three species (Factor 1). Presence of the burl, leaf length, stomatal distribution, bract marcescence, pedicel width, fruit color and mesocarp texture were the important variables separating *Arctostaphylos rainbowensis, A. peninsularis* and *A. glauca* (Factor 2).

These analyses show there is little likelihood of confusing *A. glandulosa* with any of the other three species, however, there is substantial overlap between *A. glauca* and *A. peninsularis*. Therefore, the principal components for these latter two species are plotted along with *A. rainbowensis* in Figure 4. When focusing on these species alone, there is a clear separation of all three, although the total variance explained is only 27% for Factor 1 (Table 1). The component loadings for Factor 1 indicate that the variables most responsible for separating *A. rainbowensis* from the other two species

are: burl, leaf length, branchlet and rachis indument, bract mar-cescence and mesocarp texture.

In light of the fact that 160 individuals of *A. rainbowensis* are plotted in Figures 3 and 4, it is clear that the range of variation within this species is no greater than that of *A. peninsularis, A. glauca,* or *A. glandulosa.* This pattern is also seen in the comparison of individual characters (Table 2) and is significant in addressing the hypothesis (see introduction) that *A. rainbowensis* is a hybrid pop-ulation. Hybrid populations, due to recombination and introgres-sion, typically are more variable than true-breeding species. This has been documented in manzanitas at many levels; chemistry (Ells-trand et al. 1987), physiology (Ball et al. 1983), and morphology (Keeley 1976). Based on this pattern, and the fact that *A. rainbow-ensis* is the only *Arctostaphylos* species throughout most of its range, there is little reason to treat it as a hybrid. However, as may be true for many manzanita taxa, its origin might have involved some an-cient hybridization event.

Chromosomal characteristics also reflect on the question of hy-bridization. Chromosome counts made on plants from four popu-lations throughout the range indicate that *A. rainbowensis* is diploid. For two populations we got reliable counts of $n = 13$. Although precise counts were not possible for the other two populations (be-cause of the way manzanita chromosomes stick together), they were well within the diploid range. The hypothesis that these diploid plants represent hybrids between the tetraploid *A. glandulosa* and the diploid *A. glauca* is not very compelling in light of the fact that chromosomal irregularities were not observed.

Table 2 contrasts the important characters for these four man-zanita species. Two of these characters deserve further discussion.

Some burl forming manzanita species are variable for the burl character. For example, *A. peninsularis* subsp. *peninsularis* in the Sierra San Pedro Mártir of Baja California and desert slopes of San Diego County forms burls, whereas *A. peninsularis* subsp. *juarezen-sis* in the Sierra Juárez of Baja California does not (Keeley et al. 1992). Having collected close to 500 specimens of *A. rainbowensis* from throughout its limited range we have not found any, including young saplings, that lacked burls.

The four species considered in this study differed significantly ($P < 0.01$) in stomatal distribution; stomata are equally distributed on both surfaces in two species and unequally in the other two. This character is relatively constant across the range of *A. rainbowensis* (coefficient of variation for this trait was 21%); stomatal density on the adaxial (top) side was $16–23/mm^2$ and on the abaxial side $32–40/mm^2$. In contrast, *A. peninsularis* averaged $16/mm^2$ and *A. glauca* $32/mm^2$ on both surfaces. *Arctostaphylos glandulosa* was similar to *A. rainbowensis* and averaged 26 and 41 stomata/mm^2 on the adaxial

TABLE 2. CHARACTERISTICS OF *ARCTOSTAPHYLOS* SPECIES. Quantitative characters are x̄±SD; populations with the same superscript letter are not significantly different (P > 0.05).

	A. rainbowensis	*A. peninsularis*	*A. glauca*	*A. glandulosa*
Sample size	160	70	30	30
Chromosome #	n=13	n=?	n=13	n=26
Burl	Burl	Burl/no burl	No burl	Burl
Leaves				
Length (mm)	41±0.4	29±0.5	33±1.2	37±0.9
Basal angle (°)	30[a]±9	19±11	9±8	31[a]±9
Glaucous	Weakly to intensely	Intensely	Intensely	Weakly to moderately
Scabrous	No	No	No	Yes
Stomatal ratio abaxial/adaxial	1.8±0.4	1.0[a]±0.2	1.0[a]±0.1	1.6±0.3
Branchlet indumentum	Microscopically glandular puberulent	Glabrous	Glabrous	Variously pubescent & glandular
Inflorescence				
Branches (#)	4.1±2.4	2.2[a]±1.0	2.1[a,b]±1.0	1.8[b]±0.9
Bracts				
Spacing	Spaced	Overlapping	Spaced	Overlapping
Marcescent	Strongly	Weakly	Weakly	Not
Length (mm)				
Lower	1[a]±2	2[a]±2	2[a]±3	13±2
Middle	3±1	2±1	4±1	6±2
Sepals reflexed	No	Yes	No	Yes
Fruits				
Color	Purplish-brown	Orange-red	Brown	Orange-red
Length (mm)	9.5±1.5	8.9±1.2	13.6±1.3	5.6±1.3
Ratio width/length	1.1[a]±0.6	1.0[a]±0.1	1.0[a]±0.1	1.7±0.3
Pericarp	Mealy-leathery	Papery	Papery	Very mealy
Endocarp				
Segments	Solid stone	Solid stone	Solid stone	3–5 pyrenes
Surface	Smooth	Ridges & sculpturing	Smooth	Ridges & sculpturing
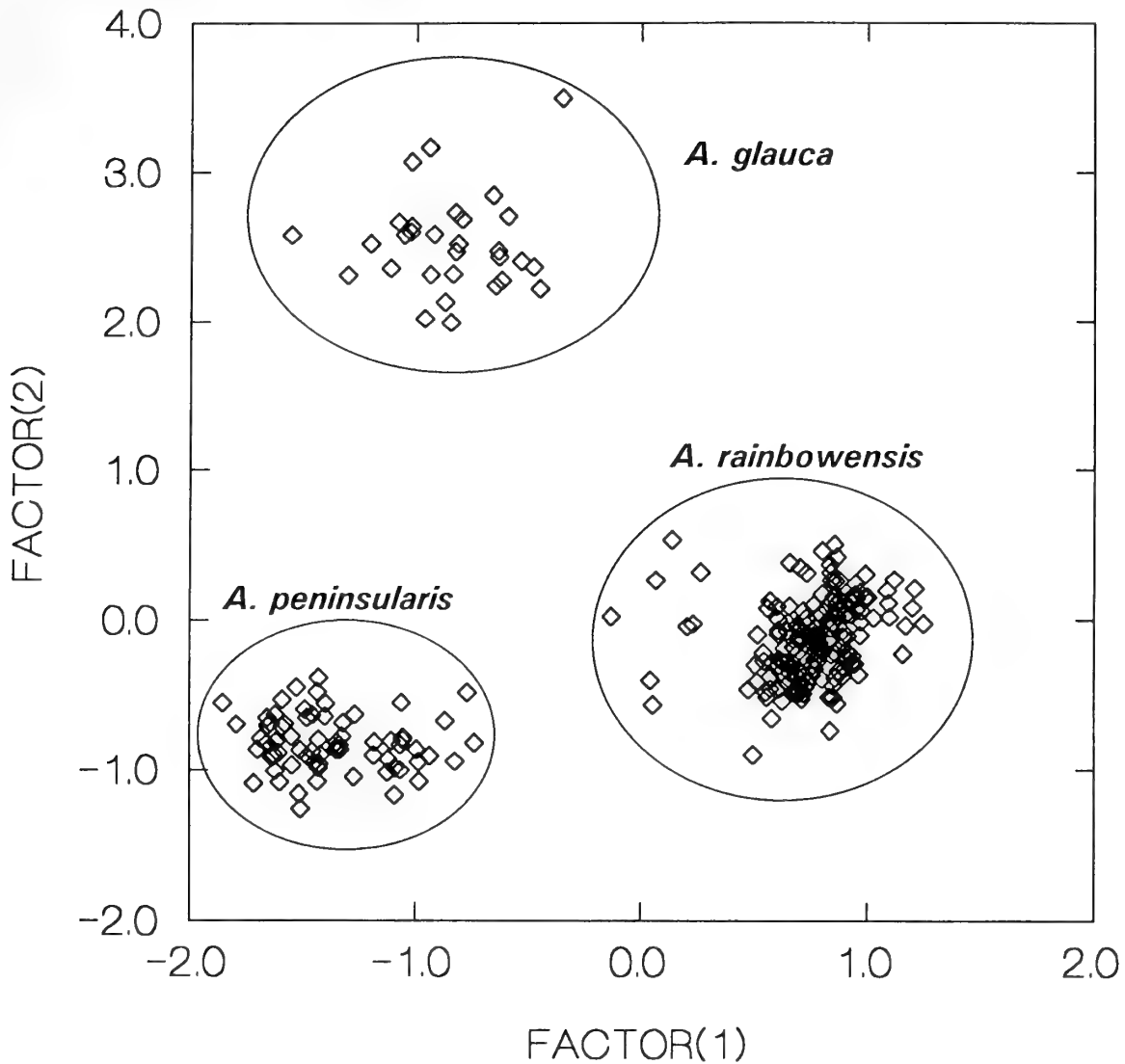
FIG. 4.   Plot of principal component analysis without *A. glandulosa*. Relative position of 260 manzanita specimens on the first two principal components of the 48 character correlation matrix. See Table 1 for factor loadings. *Arctostaphylos rainbowensis*, n = 160; *A. peninsularis*, n = 70; *A. glauca*, n = 30.

and abaxial surfaces, respectively. This agrees with the report by Howell (1945); however, Knight (1981) and Wells (1987) reported equal number of stomata on the two surfaces for *A. glandulosa*. The patterns we found support the conclusions of Howell (1945) that unequal distribution of stomata is typical of coastal manzanitas, whereas equal distribution is typical of interior species. While sto-matal distribution probably is not a highly reliable phylogenetic marker, it does suggest quite different ecophysiological modes be-tween coastal taxa such as *A. rainbowensis* and interior ones, such as *A. peninsularis*.

Based on many traits such as reduced scale-like bracts and fruits with solid stones, *A. rainbowensis* is clearly aligned with both *A. peninsularis* and *A. glauca*, and this is reflected in their alignment in Figure 3. It seems likely that these three species share a close

ancestry. Sorting out the exact phylogeny may prove to be a challenge as the high incidence of suspected hybridization in the genus (Ellstrand et al. 1987) leads to predictions of highly reticulate patterns of evolution. Certainly the manner in which these three species combine traits (Table 2) is consistent with such a model of evolution for the genus.

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THE GENUS *IBERVILLEA* (CUCURBITACEAE): AN ENUMERATION OF THE SPECIES AND TWO NEW COMBINATIONS

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Abstract

Ibervillea, a genus of tuberous perennial cucurbits of xeric environments, is closely related to *Doyerea*, *Tumamoca*, *Halosicyos*, and *Ceratosanthes*. These five New World genera, together with the African *Corallocarpus*, *Dendrosicyos*, *Kedrostis*, *Seyrigia*, and *Trochomeriopsis*, form a monophyletic lineage in the subtribe Dendrosicyinae (tribe Melothrieae), defined by the presence of tumescent seeds with reddish aril-like coverings. *Ibervillea* can be distinguished from the rest of the Dendrosicyinae by its bifid petal apices, which are infolded in bud. *Ibervillea* is currently considered to have nine species, of which two are new combinations: *Dieterlea fusiformis* becomes *I. fusiformis*, and *Corallocarpus guatemalensis* becomes *I. guatemalensis* (and is not *Doyerea emetocathartica* as suggested by previous authors).

Resumen

Ibervillea, un género de Cucurbitáceas tuberosas, perennes de ambientes xéricas, está cercana a *Doyerea*, *Tumamoca*, *Halosicyos*, y *Ceratosanthes*. Estes cinco géneros del Nuevo Mundo, juntos con los géneros Africanos *Corallocarpus*, *Dendrosicyos*, *Kedrostis*, *Seyrigia*, y *Trochomeriopsis*, forman un linea monofilética en el subtribo Dendrosicyinae (tribo Melothrieae), definada por la presencia de semillas tumescentes con cubertura rojizas como arilos. *Ibervillea* se distingue del resto de los Dendrosicyinae por los apices bífidos de los pétalos que se envuelven en boton. *Ibervillea* hoy día se considera comprender nueve especies, de los quales dos son nuevos combinaciones: *Dieterlea fusiformis* llega a ser *I. fusiformis*, y *Corallocarpus guatemalensis* llega ser a *I. guatemalensis* (no *Doyerea emetocathartica* como sugíeron previos autores).

Ibervillea Greene is one of five closely related, New World genera in the tribe Melothrieae, subtribe Dendrosicyinae (Jeffrey 1978, 1990). The five genera (*Ibervillea*, *Doyerea* Grosourdy, *Tumamoca* Rose, *Halosicyos* Mart. Crov., and *Ceratosanthes* Burm. ex Adans.) are generally found in xeric environments, have perennial, tuberous rootstocks, and fruits that turn orange or reddish at maturity. Their seeds are pyriform or spheroid, tumescent, and generally have prominent margins. A reddish aril-like flesh surrounds each seed. When the fruits are mature, birds peck holes in the brightly colored pericarp and remove the seeds, ostensibly effecting dispersal. Smaller fruits may be ingested whole. Flowers can be either nocturnal or diurnal, with species monoecious or dioecious.

This New World group of the Dendrosicyinae are closely related to the African genera *Corallocarpus* Hook. f., *Dendrosicyos* Balf. f.,

Kedrostis Medik., *Seyrigia* Keraudren, and *Trochomeriopsis* Cogn. on the basis of having tumid seeds with aril-like coverings and thecae lacking a fringe of hairs (Jeffrey 1978). The other New World Dendrosicyinae (*Apodanthera* Arn., *Cucurbitella* Walp., *Guraniopsis* Cogn., *Melothrianthus* Mart. Crov., and *Wilbrandia* Manso) also lack hair on the thecae, but have seeds which are somewhat flattened and which lack the reddish, aril-like covering. In addition, the fruits of this latter group are often ribbed or slightly sulcate, in contrast to the smooth fruits of *Ibervillea* and more closely related genera. The exact relationship between the African and New World "arillate" Dendrosicyinae awaits further study.

Following a key to the five closely related New World Dendrosicyinae, a review to the nomenclature of *Ibervillea* is presented. Some names used in recent floristic accounts (Correll and Johnston 1970; Hatch et al. 1990; Johnston 1990; Lira 1988) are now considered to be synonyms or misapplied and two new combinations are made. Although a complete revision of *Ibervillea* is in progress (Kearns and Lira in prep.), the nomenclatural changes are presented now, so they may be used in upcoming floristic treatments.

KEY TO *IBERVILLEA* AND RELATED NEW WORLD GENERA IN THE DENDROSICYINAE

1. Flowers rotate to broadly campanulate, <5 mm wide; plants dioecious; both staminate and pistillate flowers in dense glomerate clusters (extremely compacted racemes), often appearing on leafless stems; fruits oblong, in dense clusters, 1–2 cm long .... *Doyerea*
1'. Flowers elongate-funnelform, salverform to campanulate-salverform, mostly >5 mm wide and up to 50 mm wide; plants monoecious or dioecious; staminate flowers in racemes with long peduncles (occasionally compacted), pistillate flowers solitary or racemose, appearing with leaves (on leafless stems in some *Ceratosanthes*); fruits globose, oblong, or fusiform, solitary or racemose, (1–)2–15 cm long, when small, then globose.
    2. Petals infolded or inrolled in bud, with bifid apices (entire in *Ibervillea fusiformis*), densely or sparsely pubescent.
        3. Petal lobes long and narrow, inrolled in bud; petal margins entire; hypanthia narrowly funnelform; female flowers in racemes or solitary, with 2 style branches and placentae; often flowering when leafless, dioecious or monoecious .... *Ceratosanthes*
        3'. Petal lobes short and broad, infolded in bud; petal margins undulate; hypanthia campanulate to cylindrical; female flowers always solitary, with 3–5 style branches and placentae; flowers always appearing with leaves, dioecious .... *Ibervillea*
    2'. Petals valvate in bud, with entire apices, lightly papillate or glabrous.
        4. Plants dioecious; petals lightly papillate, with rounded apices; hypanthia campanulate-cylindrical; styles 2-branched; seeds with prominent margins and smooth surfaces .... *Halosicyos*
        4'. Plants monoecious; petals glabrous, with acute apices; hypanthia narrowly elongate-funnelform; styles 3-branched; seeds with obscure margins and rugose surfaces .... *Tumamoca*

Ibervillea Greene, Erythea 3:75. 1895.—TYPE SPECIES: *Ibervillea lin-*
dheimeri (A. Gray) Greene. *Maximowiczia* Cogn. in A. & C.
DC., Monogr. Phan. 3:726. 1881, non Ruprecht 1856. *Dieterlea*
E. J. Lott, Brittonia 38:407. 1986., syn. nov.

Climbing, dioecious perennials of xeric environments; rootstocks
tuberous; stems perennial or annual; tendrils simple. Leaves slightly
lobed to highly divided, lacking leaf glands; lobes broad to narrow.
Inflorescences of male flowers in racemes (occasionally congested),
and female flowers solitary. Flowers 8–60 mm long; petals yellow
(whitish in *I. fusiformis* [E. J. Lott] Kearns), clawed, densely pu-
bescent inside, with broadly bifid apices infolded in bud (entire in
I. fusiformis); margins undulate; stamens 3 (2 bithecal, 1 monoth-
eceal) free to tightly connivent; thecae 5, straight. Fruits fleshy ber-
ries, globose to fusiform or oblong, green with linear arrays of white
spots when young, turning dark orange at maturity. Seeds many,
tumescent, with prominent margins, enveloped by a red or orange
fleshy aril-like covering, apparently dispersed by birds. 9 species.

Ibervillea is found in the southwestern United States (Texas, New
Mexico, Arizona), throughout the drier regions of Mexico and Belize,
and in the dry central valley of southern Guatemala. All nine species
occur in Mexico.

1. **Ibervillea fusiformis** (E. J. Lott) Kearns, comb. nov. *Dieterlea*
fusiformis E. J. Lott, Brittonia 38:407. 1986.—TYPE: MEXICO,
Jalisco: Mpio. La Huerta, Estación de Biología Chamela
U.N.A.M., Vereda El Tejón, 800 m, 17 Jul 1984. *Magallanes*
4252 (holotype: MEXU; isotypes: CAS, ENCB, MICH!, MO!,
NY!).

Representative specimens. MEXICO, COLIMA: Municipio Man-
zanilla, Los Periquillas, 19 Jan 1986, *Lott 2754* (NY). JALISCO:
Hwy 200, 3.8 mi N of road to Tomatlan, 9 Sep 1985, *Kearns 258*
(MEXU, TEX); SE of Estación de Biología Chamela (UNAM), 9
Sep 1983, *Lott 1849* (MEXU). SINALOA: Cerros del Fuerte, 18–
24 mi N of Los Mochis, 25 Sep 1954, *Gentry 14290* (US). SONORA:
14.2 mi N of Alamos on road to San Bernardo, 27 Aug 1985, *Kearns*
196 (MEXU, TEX).

Study of *Ibervillea*, including newly discovered species and ad-
ditional collections of poorly-known taxa, has led to the conclusion
that *Dieterlea* E. J. Lott does not merit recognition as a separate
genus and that the single species must be positioned in *Ibervillea*.
Dieterlea was established (Lott 1986) for a species (herein recognized
as *I. fusiformis*) from Jalisco with large yellowish-white, nocturnal
flowers and large fruits. Although closely related, Lott separated
Dieterlea from *Ibervillea* by its perennial stems, much larger white

nocturnal flowers, connate anthers, four or five placentae, four or five bilobed stigmas, and five staminodia. These characters, however, are now known to occur in some species of *Ibervillea*.

Ibervillea fusiformis is aligned with the group consisting of *Ibervillea maxima* Lira & Kearns, *I. hypoleuca* (Standl.) C. Jeffrey, and *I. guatemalensis* (Standl. & Steyerm.) Kearns. These species also have perennial stems, large fruits, branched rootstocks, and a similar leaf pubescence. The only closely related species for which we have good pistillate material, *I. maxima,* also has five placentae and stigmas. Other species of *Ibervillea,* such as *I. tenuisecta,* have three placentae and stigmas. All species of *Ibervillea* investigated have five staminodia.

Lott also considered connate anthers as a distinguishing feature of *Ibervillea fusiformis.* The anthers of this species, however, can be teased apart with a dissecting needle (in FAA-preserved flowers). The anthers of *I. guatemalensis* are almost as closely adherent, thus also appearing fused, whereas other species of *Ibervillea* have completely free anthers. Although the anthers of *I. fusiformis* are more tightly adherent than those of the other species of *Ibervillea,* this character state is merely an extreme of a continuum and does not represent a disjunct evolutionary development.

Not all species of *Ibervillea* have diurnal flowers. The flowers of *I. fusiformis* bloom late at night, well after sunset (ca. 12:00 midnight), and close in early morning, after dawn. Those of *I. maxima* also open at night (ca. 9–11:00 p.m.), but remain open during the following day. *Ibervillea guatemalensis* and *I. hypoleuca* flowers open before dawn (sometime between 3:30 and 6:30 a.m.) and close in the early afternoon. The flowers of *I. lindheimeri, I. tenuisecta,* and *I. sonorae* (S. Wats.) Greene all open in the early morning, after dawn, and close in the afternoon. Given the variation in the timing of anthesis in the other species of *Ibervillea,* there is no reason to segregate *I. fusiformis* on the basis of nocturnal flowering.

One qualitative distinction between *Ibervillea fusiformis* and the rest of the genus is in the nature of the petal apices. For all species of *Ibervillea* except *I. fusiformis,* the petal apices are broadly bifid. The petal apices of *I. fusiformis,* however, are entire, the difference possibly in response to the presumed pollinators, sphingid moths (Lott 1986). The pollinators of other species of *Ibervillea* are bees (diurnal-flowering plants) or unknown (nocturnal-flowering plants).

Other than those discussed above, the characters which clearly place *Dieterlea* within *Ibervillea* include densely pubescent clawed petals with ruffled margins. Although the large yellow-white flowers of *Dieterlea* appear quite different from the small yellow flowers of some species of *Ibervillea,* the female flowers of *I. maxima* are only slightly more yellow in color than the flowers of *I. fusiformis.* A

comparison of all species of *Ibervillea* clearly demonstrates that *Dieterlea* can no longer be maintained as a separate genus.

2. *Ibervillea maxima* Lira & Kearns, Sida 14:223–226. 1990.—TYPE: UNITED STATES, Texas: cultivated in Austin 1986–1989 using seed from *Kearns and Kearns 390,* Nayarit, Mexico, along W side of hwy 15 at km 39, 140 m, 27 Mar 1986, *Kearns C-390* (holotype: MEXU!; isotypes: BM!, BRIT!, CHAPA!, CAS!, ENCB!, F!, GUAD!, IBUG!, K!, MICH!, MO!, NY!, TEX!, UC!, US!, XAL!).

Representative specimens. MEXICO, JALISCO: near Zapotlan, 27 May 1893, *Pringle 5504* (MICH, NY, US); Sierra de San Juan, San Juan Cosala, 8 Jul 1974, *Díaz 5251* (MICH). NAYARIT: Mirador de Aguila, 14 km N of Tepic, 10 Jul 1957, *McVaugh 15292* (MICH); 8 mi E of San Blas, 7 Nov 1961, *Gentry 19479* (US). SINALOA: Foothills of the Sierra Madre, 14 July 1897, *Rose 1659* (NY, US).

Plants from which the type material was obtained are still under cultivation in the author's living collection (currently in St. Louis). Since one previously sterile specimen has finally started to produce pistillate flowers, there will be an opportunity in the future to provide pistillate material as an adjunct to the staminate type specimens.

3. *Ibervillea hypoleuca* (Standl.) C. Jeffrey, Kew Bull. 33:349. 1978. *Corallocarpus hypoleucus* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 17:223. 1937.—TYPE: MEXICO, Guerrero: south of Acapulco, on road near La Sabana, 60 m, 25 Aug 1935. *MacDaniels 266* (holotype: F!, photo K!).

Representative specimens. MEXICO, JALISCO: 16 km N of Cuidad Guzmán, 13 Nov 1971, *Dieterle 4182* (MICH); 5.6 mi N of Tecalitlan, 3 Oct 1986, *Kearns 463* (MEXU, TEX); Bahia Tenacatita, between Bahia Navidad and La Manzanilla, 12 Nov 1960, *McVaugh 21018* (MICH). MICHOACAN: 15–16 km SE of Asserradero Dos Aguas, 25–26 Nov 1970, *McVaugh 24728* (MICH); road to Jiquilpan, 3 km E and 8–10 km NE of Cotija de la Paz, 1 Dec 1970, *McVaugh 24907* (MICH).

4. **Ibervillea guatemalensis** (Standl. & Steyerm.) Kearns, comb. nov. *Corallocarpus guatemalensis* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. 23:93. 1944.—TYPE: GUATEMALA, ZACAPA: vicinity of Zacapa, 200 m, Oct 1940, *Standley 74623* (holotype: F!, photo K!). PARATYPE: GUATEMALA, CHIQUIMULA: along gorge of Río Chiquimula, between Santa Bárbara and Petapilla, 4–6 mi N of Chiquimula, 350–420 m, *Steyermark 30258* (F).

Representative specimens. GUATEMALA, EL PROGRESSO: Hwy 9, 7 mi E of road to El Rancho, 14 Nov 1986, *Kearns 516* (MEXU, TEX); ZACAPA: between Zacapa and Chiquimula, 14 Nov 1986, *Kearns 519,* (MEXU, TEX). MEXICO, CHIAPAS: Trapichito, Comitan, 2 Jun 1945, *Matuda 5692* (MEXU).

Corallocarpus guatemalensis was described from sterile material collected in the dry central portion of southern Guatemala. Dieterle (1976) treated this as a synonym of *Doyerea emetocathartica* in her treatment of the Cucurbitaceae for the Flora of Guatemala, as did Jeffrey (1978) in his overview of the New World cucurbits. Collection and subsequent cultivation of rootstocks from the type locality (*Kearns 516, 519*) has led to the unmistakable conclusion that the previously available (sterile) specimens of *C. guatemalensis* were misidentified as *D. emetocathartica.* Given flowering material, it is obvious that Standley and Steyermark's plant is a species of *Ibervillea.* The taxon is noteworthy for having long, horizontally-oriented rootstocks. The type locality is situated in an area of serpentine soils. *Ibervillea guatemalensis* is closest to *I. hypoleuca* and *I. maxima,* sharing similar leaf pubescence, perennial stems with lenticels, and staminate floral structure. A complete description of this species will appear in the forthcoming revision of the genus (Kearns and Lira in prep.).

5. *Ibervillea millspaughii* (Cogn.) C. Jeffrey, Kew Bull. 33:348–349. 1978.
    Corallocarpus millspaughii Cogn., Publ. Field Mus. Nat. Hist., Bot. Ser. 1:322, t. 20. 1896.—TYPE: MEXICO, Yucatan: near Izamal, *Gaumer 842* (syntypes: F, NY!, photo K!).

Representative specimens. MEXICO, VERACRUZ: Municipio Alvarado, 15 km NW of Alvarado, 3 Jan 1986, *Andres 172* (MICH, MO, NY, TEX); Tampico, 7 June 1910, *Palmer 500* (US). YUCATAN: forest of Suitun, May 1916, *Gaumer 23290* (NY); Merida, *Sousa 410* (MEXU, US). BELIZE, COROZAL DISTRICT: San Andres, Dec 1933, *Gentle 1088* (MICH, NY).

6. *Ibervillea lindheimeri* (A. Gray) Greene, Erythea 3:75. 1895.
    Sicydium lindheimeri A. Gray, Pl. Lindh. 2:194. 1850. *Maximowiczia lindheimeri* (A. Gray) Cogn., DC. Monogr. Phan. 3:727. 1881.—TYPE: UNITED STATES, Texas: Comal Co: Comanche Springs, New Braunfels, 1850, *Lindheimer 612* (holotype: GH, isotype: K!, MO!).
    Bryonia abyssinica Gouault, Rev. Hort. 1853:61. 1853. non Lam. 1785.
    Sicydium tenellum Naud., syn. nov., Ann. Sci. Nat. 4(16):167., pl. 1. 1862. *Maximowiczia tripartita* var. *tenella* (Naud.) Cogn.

in A. & C. DC. Monogr. Phan. 3:727. 1881. *Ibervillea tenella* (Naud.) Small, Fl. Southeastern U.S.A. 1136. 1903.—TYPE: FRANCE, Paris: cultivated in Botanic Garden from Texas seed sent by Victor Considérant, *Naudin s.n.* (holotype: P).

   Sicydium tripartitum Naud., syn. nov., Ann. Sci. Nat. 4(16):166. 1862. *Maximowiczia tripartita* (Naud.) Cogn. in A. & C. DC. Monogr. Phan. 3:727. 1881. *Ibervillea tripartita* (Naud.) Greene, Erythea 3:75. 1895.—TYPE: FRANCE, Paris: cultivated in Botanic Garden from Texas seed sent by Victor Considérant, *Naudin s.n.* (holotype: P, photo: F, MICH!).

Representative specimens. UNITED STATES, TEXAS, Bell Co.: near Salado, 23 June 1930, *Wolff 2319* (US). Brazos Co.: College Station, 23 April 1918, *Palmer 13431* (MO, US). Calhoun Co.: Farewell Island, 22 May 1930, *Tharp s.n.* (MICH, MO, NY, TEX, UC). Kerr Co.: Kerrville, 3 May 1894, *Heller 1694* (MO, NY, UC, US). San Saba Co.: San Saba, 5 May 1917, *Palmer 11823* (MO, NY, US).

The listing of *Bryonia abyssinica* Gouault as a synonym of *Ibervillea lindheimeri* requires some explanation. In an account for Revue Horticole, Gouault (1853) misidentified a specimen of *I. lindheimeri* that he had growing in his garden as *B. abyssinicia* Lam. Although the name he had chosen was wrong, Gouault correctly attributed its authorship to Lamarck. *Bryonia abyssinica* subsequently appeared in Index Kewensis and in Monographie Phanerogamarum (Cogniaux 1881) as a synonym of *I. lindheimeri* (as *Maxicmowiczia*), the authorship incorrectly attributed to Gouault. Cogniaux did note Lamarck's usage, but Gouault did not intend to describe a new taxon when he used Lamarck's species to identify his specimen of *Ibervillea*. Thus, Gouault's mistaken identification of *I. lindheimeri* entered the literature via a bibliographic mistake and is not a later homonym in the strict sense. *Bryonia abyssinica* is a synonym of *Coccinia abyssinica* (Lam.) Cogn. (Cogniaux 1881).

Naudin distinguished *Ibervillea tenella* and *I. tripartita* from *I. lindheimeri* largely on the basis of leaf shape and number of flowers per inflorescence, a conclusion derived from an inadequate sampling of the morphological diversity in *I. lindheimeri,* under which Naudin's species must be placed. The specimens cultivated by Naudin exemplify the variation among populations of *I. lindheimeri.* An examination of numerous *Ibervillea* collections from Texas indicates that there are only two resident species: *I. tenuisecta* in western Texas and *I. lindheimeri* in the central and eastern part of the state. Leaf shape in *I. lindheimeri* is quite variable and leaf segments tend to be narrower in the southern part of the state, resulting in some specimens being misidentified as *I. tenuisecta. Ibervillea lindheimeri* has globose seeds with hypogeal germination and uniseriate petal

trichomes, whereas *I. tenuisecta* has more flattened (but still tumescent) seeds with epigeal germination and shorter, capitate petal trichomes. For most populations, the fruits of *I. tenuisecta* are considerably smaller than those of *I. lindheimeri.*

7. *Ibervillea sonorae* (S. Watson) Greene, Erythea 3:75. 1895.

Maximowiczia sonorae S. Watson, Proc. Amer. Acad. Arts 24: 51. 1889.—Type: MEXICO, Sonora: Guaymas, 1887, *Palmer 283* (holotype: GH, isotypes: K!, NY!, US!).

Maximowiczia insularis Brandegee, Univ. Calif. Publ. Bot. 6:361. 1916. *Maximowiczia sonorae* var. *brevicaulis* (T. Brandegee) I. M. Johnston, Proc. Cal. Acad. Sci. 4(12):1179–1180. 1924. *Ibervillea insularis* (Brandegee) Wiggins, Flora of Baja California. 391. 1980.—Type: MEXICO, Baja California: Magdalena Bay, 15 Jan 1889, *Brandegee s.n.* (holotype: UC #102050!).

Maximowiczia sonorae var. *peninsularis* I. M. Johnston, Proc. Cal. Acad. Sci. 4:1178. 1924. *Ibervillea sonorae* var. *peninsularis* (I. M. Johnston) Wiggins, Flora of Baja California. 391. 1980.— Type: MEXICO, Ceralbo Island, Gulf of California, on a sandy point just north of Gordas point, 6 Jun 1921, I. M. *Johnston 4026* (holotype: CAS!).

Ibervillea guarequi MacDougal, nom. nud. in Old and New Plant Lore, Smithsonian Series 11:278–279. 1931. Name and note only, not formally described. The attribution of the specific epithet was possibly an editing mistake, as "guarequi" is a common name for this species.

Representative specimens. MEXICO, BAJA CALIFORNIA SUR: Rancho Aguajito, Arroyo Gua, NW of Loreto, 26 Sep 1967, *Carter & Moran 5253* (UC, US); Santa Margarita Island, 20 Mar 1911, *Rose sn* (NY, US). SINALOA: Bahia Topolobampo, 5 Jan 1952, *Gentry 11449* (MICH). SONORA: 2 mi NE of San Carlos, 40 mi W of Hermosillo, 30 Aug 1941, *Wiggins & Rollins 185* (MICH, MO, NY, UC); 6.9 mi SE of Cuidad Obregon, 12 Sep 1973, *Stevens 2074-A* (MICH, MO).

8. *Ibervillea tenuisecta* (A. Gray) Small, Fl. Southeastern U.S. 1136, 1138. 1903.

Sicydium lindheimeri var. *tenuisectum* A. Gray, Pl. Wright. 1:75. 1852. *Maximowiczia lindheimeri* var. *tenuisecta* (A. Gray) Cogn., in DC., Monogr. Phan. 3:728, 1881.—Type: UNITED STATES, New Mexico: near the Rio Grande, 1851, *Wright 221* (holotype: GH, isotype: K!).

Representative specimens. MEXICO, CHIHUAHUA: 20 mi E of Chihuahua City, 1 Aug 1949, *Freytag M93* (MEXU, MO). COA-

HUILA: 40 km S of Puerto del Gallo, 9 Aug 1973, *Johnston, Wendt & Chiang 12168* (MEXU, TEX). DURANGO: 63 km E of Ceballos, 7 Sep 1983, *Torres 3597* (MEXU, MO, NY). USA, TEXAS, Hudspeth Co.: 3.5 mi N of Acala, 31 Oct 1962, *Correll 26580* (TEX, UC). NEW MEXICO, Sierra Co.: Rio Grande, 30 mi N of Rincon, 5 Sep 1904, *Metcalfe 1289* (MO, NY, UC, US).

9. *Ibervillea* sp.

Representative specimens. MEXICO, OAXACA: 6 km NE of Tehuantepec, 5 July 1959, *King 1333* (MICH, NY). VERACRUZ: Municipio Dos Ríos, La Cumbre, 3 Aug 1971, *Ventura 4003* (MICH); Municipio Puente Nacional, Tamarindo, 22 Jun 1971, *Ventura 3727* (MICH). YUCATAN: km 28, Mérida-Progresso road, 28 Jun 1971, *Stevens 1141* (MICH); Izamal, Jun 1916, *Guamer 23373* (NY).

Collections of an *Ibervillea* with crenate leaf margins from southern Mexico have been misidentified as *I. tripartita* (Lira, 1988; Standley, 1930). Because *I. tripartita* is a later name for *I. lindheimeri,* this Mexican species is without a legitimate name. A full description will be included in a forthcoming treatment of the genus (Kearns and Lira in prep.).

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ANNOUNCEMENT

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3–5 June 1994

Valley Life Sciences Building,
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Friday, 3 June
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.... Lincoln Constance

Saturday, 4 June
Morning Symposium
Future of Plant Systematics, Science, and Society ...... Brent Mishler
Flowers in the Garden: What Next for California Floristics? ....
.... Dieter Wilken
Cooperation and Collaboration: Herbaria and Botanical Gardens
.... George Rogers
Rarity in California .... Peggy Fiedler
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A REVISION OF *TUMAMOCA* (CUCURBITACEAE)

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ABSTRACT

Tumamoca is a small genus of perennial North American cucurbits related to *Ibervillea, Ceratosanthes, Doyerea,* and *Halosicyos* (tribe Melothrieae, subtribe Dendrosicyinae). *Tumamoca,* previously considered monotypic, is now known to have two species, *T. macdougalii* of the Sonoran Desert and the here described *T. mucronata* from northern Mexico.

RESUMEN

Tumamoca, un genero pequeño de Cucurbitáceas Norteamericanas, está mas cerca a *Ibervillea, Ceratosanthes, Doyerea,* y *Halosicyos* (tribe Melothrieae, subtribo Dendrosicyinae). Antes de esta revisión, *Tumamoca* estaba monotypica, ahora sabemos que hay dos especies, *T. macdougalii* del Desierto de Sonora y la especie, nueva, *T. mucronata* desde Mexico norteño.

Review of herbarium collections at TEX, in conjunction with the Flora of Mexico project, has uncovered a new species of *Tumamoca* Rose from the Chihuahuan Desert region of northern Mexico. Along with the description of the new species, a revision of the entire genus is presented.

Tumamoca is part of a closely related group of New World cucurbits (tribe Melothrieae, subtribe Dendrosicyinae), which includes *Ibervillea* Greene, *Ceratosanthes* Burm. ex Adans., *Doyerea* Grosourdy, and *Halosicyos* Mart. Crov. (Jeffrey 1990). Plants of these genera are perennials with tuberous rootstocks, tend to grow in xeric environments, and have fruits which turn orange or reddish at maturity. Their seeds are pyriform or spheroid, tumescent, and generally have prominent margins. A reddish aril-like flesh surrounds each seed. When the fruits are mature, birds peck holes in the brightly colored pericarp and remove the seeds, ostensibly effecting dispersal. Smaller fruits may be ingested whole. Flowers can be either nocturnal or diurnal, with species monoecious or dioecious. Generic boundaries are currently based on aspects of floral morphology (Kearns 1994).

The genus *Tumamoca* was established by Rose (1912) for a small perennial cucurbit that resembled a delicate *Ibervillea.* This "curious little cucurbit" grew over the low shrubs around the Desert Laboratory of the Carnegie Institution near Tucson. Rose chose the generic name to commemorate Tumamoc Hill, the Amerindian name

of the hill on which the Desert Laboratory was situated. *Tumamoca* was separated from *Ibervillea* by its monoecious vines, very slender "calyx tube" (hypanthium), roughened emarginate seeds, and clustered tuberous roots.

The characters used by Rose to separate *Tumamoca* from *Ibervillea* are still valid (with a couple of exceptions) and additional distinctions can be made between the two genera. The exceptions to Rose's criteria include the occurrence of clustered roots in some species of *Ibervillea* and the roughened seeds of *I. sonorae* (S. Watson) Greene. In addition to the characters listed by Rose, *Tumamoca* is distinguished by having three staminodia, entire petals, glabrous interior corolla surfaces, and valvate buds. *Ibervillea* has five staminodia, petals with bifid apices and pubescent interior surfaces, and buds with infolded apices.

Tumamoca Rose, Contr. U.S. Natl. Herb. 16:21, pl. 17. 1912.—
    Type Species: *T. macdougalii* Rose.

Small delicate, perennial, monoecious vines, with branched, tuberous rootstocks. Tendrils simple. Leaves deeply 3–parted, with lobes once or twice parted, the segments narrow. Flowers salverform, pale yellowish, glabrous, opening at night, with elongate, narrow hypanthia and small sepals; petals narrowly triangular, entire, valvate in bud. Staminate flowers almost sessile, in racemes; stamens free, 3 (2 bithecal + 1 monothecal); anthers sessile, attached at top of hypanthium tube, with glabrous appendages at apex and base; thecae straight. Pistillate flowers solitary, from same leaf axils as staminate inflorescences; styles long, 3-fid, with long coiled stigmas; staminodia 3, small, level with branching of style. Fruits glabrous, fleshy berries, reddish or yellowish; seeds few, black, obovoid, with a rough testa and obscure margins.

Distributed from the southwest United States to northern Mexico in xeric environments.

Key to the Species of *Tumamoca*

1. Leaf segments 2–10 mm wide; lower leaf surface with many very short hairs with well-developed multicellular bases (0.2–0.3 mm wide); hypanthia of staminate flowers 5–9 mm long; sepals triangular; pistillate flowers with peduncle 5–15 mm long .... 1. *T. macdougalii*
1'. Leaf segments 0.5–2 mm wide; lower leaf surface sericeous, with hairs lacking multicellular bases; hypanthia of staminate male flowers ca. 14 mm long; sepals rounded, mucronate; pistillate flowers with peduncle 2–5 mm long ....
    .... 2. *T. mucronata*

1. *Tumamoca macdougalii* Rose (Fig. 1), Contr. U.S. Natl. Herb.
    16:21., pl. 17. 1912.—Type: UNITED STATES. Arizona: Tuc-
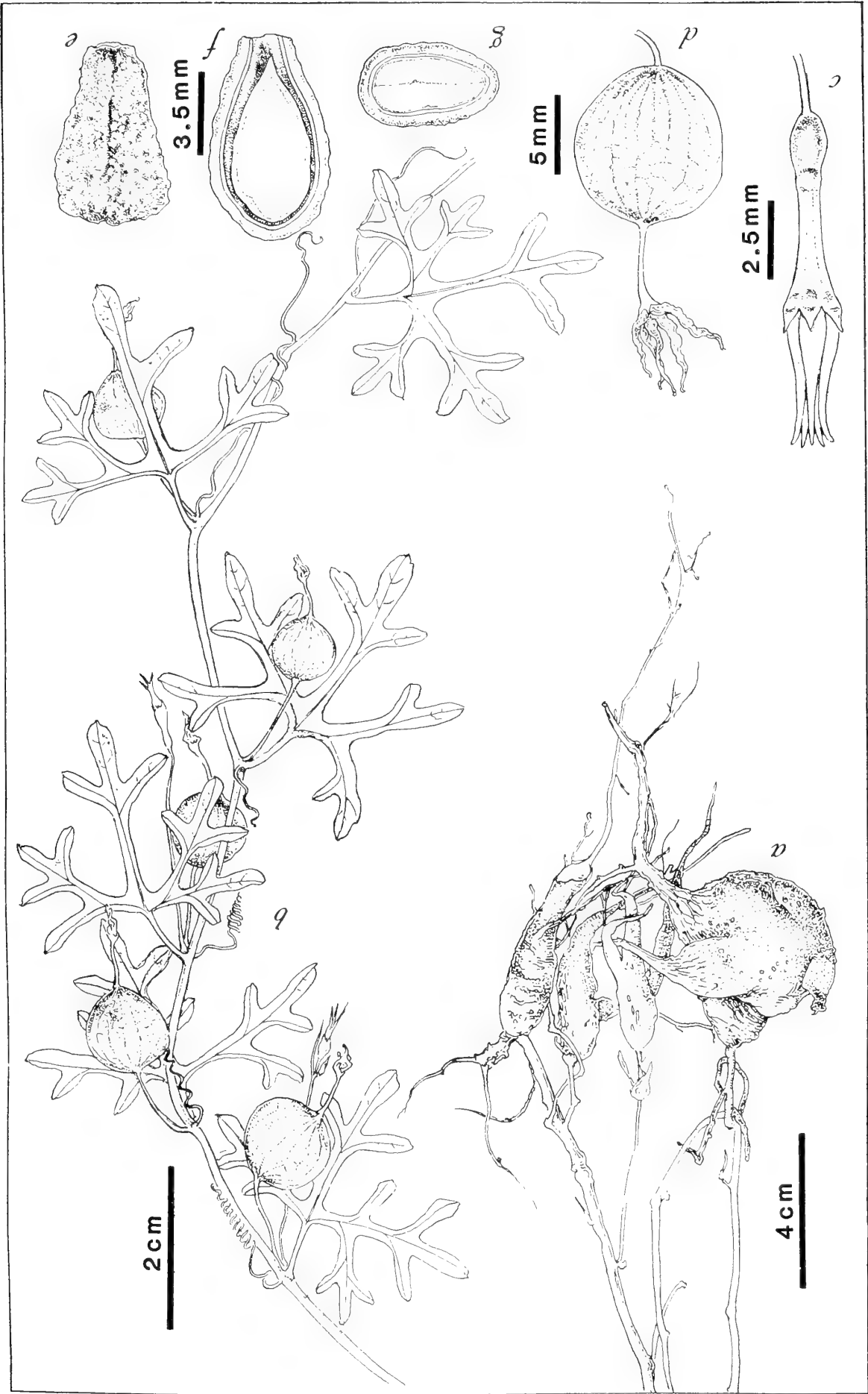
FIG. 1.   *Tumamoca macdougalii* Rose. copied from Rose (1912). a. roots; b. fruiting branch; c. staminate flower; d. fruit; e. seed; f. seed, longitudinal section; g. seed, cross-section.
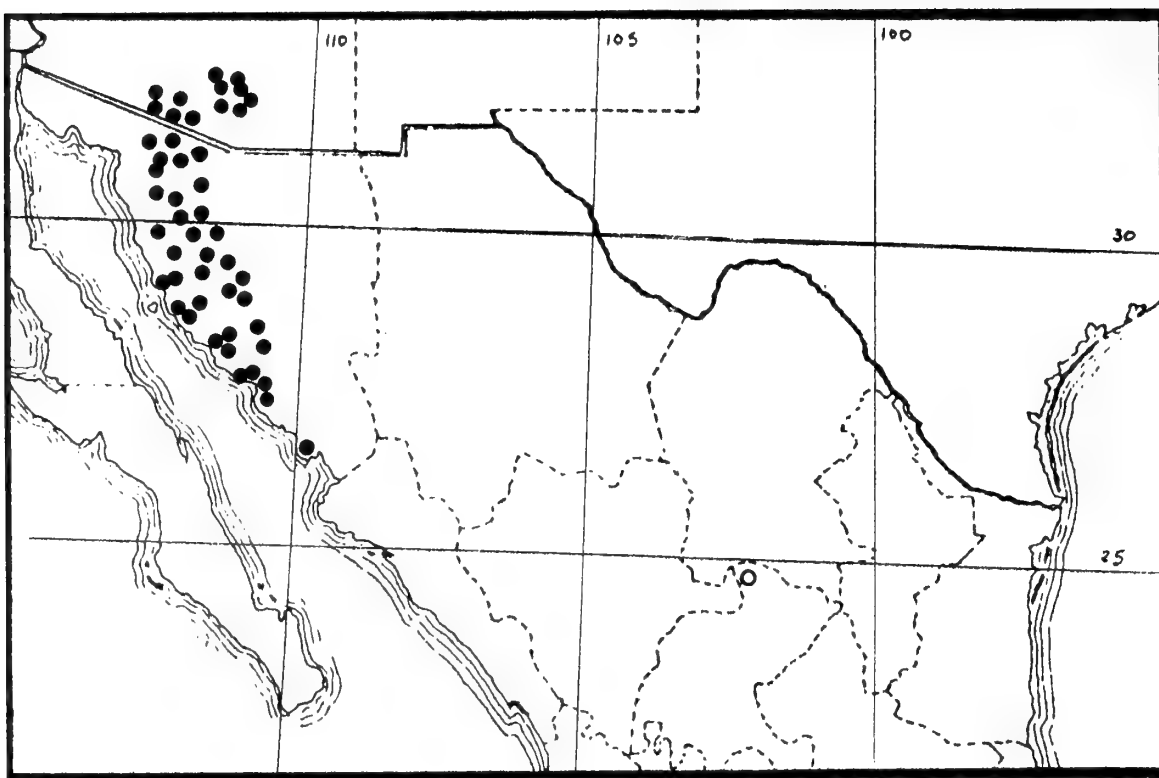
Fig. 2. Distribution of *Tumamoca*. ● = *T. macdougalii* in Arizona and Sonora, and ○ = *T. mucronata* in Zacatecas. Addtional locations of *T. macdougalii* from Reichenbacher (1990).

son, collected near the Desert Laboratory, 31 Jul 1908, *MacDougal s.n.* (holotype: US accession # 591589!).

Stems glabrous, internodes 3–4 cm long. Leaves to 4.5 cm long, with segments 2–10 mm wide, upper surface glabrous, lower surface with very short hairs (<0.1 mm long) with well-developed multi-cellular bases (0.2–0.3 mm wide); petioles 1–2 cm long. Staminate flowers in racemes 3.5–10 cm long, with 2–19 flowers; peduncles 10–25 mm long (or longer); hypanthium 5–9 mm long and 1.3–1.7 mm wide at top; sepals triangular, 0.5–1 mm long, 0.3–0.7 mm wide; petals 4–4.5 mm long. Female flowers with peduncles 5–15 mm long; hypanthium 5.5–7.5 mm long, 1.5 mm wide at top; sepals 0.3–1 mm long, 0.7 mm wide; petals 5–6 mm long; ovary 4.5 mm long, 2 mm wide. Fruits red, rarely yellow at maturity, globose, 8–10 mm in diameter; seeds ca. 7 mm long, ca. 4.5 mm wide, ca. 3 mm thick.

Distributed from southern Arizona, United States, to Sonora, Mexico, at elevations below 1000 m, in Sonoran desert scrub, Sinaloan thornscrub, and Semidesert grassland (Fig. 2). The roots are said to smell like decaying cabbage when bruised. Javelina uproot and eat the succulent tuberous roots (Reichenbacher 1990).

The "Tumamoc globeberry" has been included on the Federal List of Endangered and Threatened Plants, but recent study has

shown that the species is more common and widespread than previously thought (Reichenbacher 1990). Given this clearer understanding of the distribution, a proposal is in process to remove *Tumamoca macdougalii* from the Federal list of protected species (Rutman 1992).

Additional specimens examined. MEXICO: Sonora: 10–15 m E of Empalme along rd to Cd. Obregon, 5 Sep 1974, *Gentry & McClure 23442* (US); S of Huatabampo on the road to Huatabampo, 0.25 mi NE of Maroncarit, 4 Sep 1989, *Sanders et al. 9246* (MO, TEX); Sierra de la Nariz & Sta. Magdalenas, 25 July 1855, *Schott sn.* (NY); 1.5 mi N of Kino Bay, 29 Aug 1941, *Wiggins & Rollins 163* (MICH, MO, NY); 5 mi N of Suboural, 3 Sep 1941, *Wiggins & Rollins 263* (MO); junction of road to Horcasitas with old hwy on rr 6 mi S of Carbo, 16 Sep 1934, *Wiggins 7273* (MICH, US).

UNITED STATES: Arizona: Pima Co., Quijotoa region, 24 Sep 1943, *Gooding & Reeder M22-43* (NY); 4 mi S of Mission San Xavier, 23 Aug 1941, *Wiggins & Rollins 46* (MO, UC, US); W of Mission road near the base of Black Mountain, San Xavier Indian Reservation, 2600 ft, 3 Sep 1984, *Lapre & Boyd s.n.* (UC); Sells-Ajo hwy N of Gunsight, 24 Sep 1943, *Godding & Reeder s.n.* (MICH); near Desert Laboratory, Tucson, 4–23 Oct 1910, *MacDougal s.n.* (US); cultivated in Austin, Texas, from seed collected near Tucson, Ariz., *Kearns C-THS59* (living plants).

2. **Tumamoca mucronata** Kearns, sp. nov. (Fig. 3).—TYPE: MEXICO. Zacatecas: near and at Sierra del Yeso, almost due west of La Prensa de Los Angeles, 1400–1500 m, 30 Jun 1973, *Johnston, Wendt, & Chiang 11525A* (TEX!).

T. macdougalii Rose similis sed habitatione gypseo, foliis divisionibus angustatis, floribus majoribus, floribus feminenis in pedunculis brevioribus, et sepalis rotundatis mucronatisque.

Stems with scattered stiff uniseriate hairs, internodes 3–5 cm long. Leaves to 3.5 cm long, with very narrow segments (0.5–2 mm wide), upper surface with scattered uniseriate hairs, usually with small multicellular bases, lower surface sericeous, with hairs lacking multicellular bases; petioles ca. 1 cm long. Staminate flowers in inflorescences 4–5 cm long, with 7–10 (or more?) flowers; peduncles 25–30 mm long; hypanthium ca. 14 mm long and 1.5–2 mm wide at top; sepals rounded, mucronate, 0.8–0.9 long (including mucro), 0.6–0.8 mm wide; mucro 0.2–0.3 mm long; petals 5–6 mm long. Pistillate flowers with peduncles 2–5 mm long; hypanthium 9 mm long, 1 mm wide at top; sepals 0.7 mm long (including mucro), 0.5 mm wide; petals 4 mm long; ovary fusiform, glabrous, ca. 2.5 mm long (possibly longer at anthesis). Mature fruits unknown.
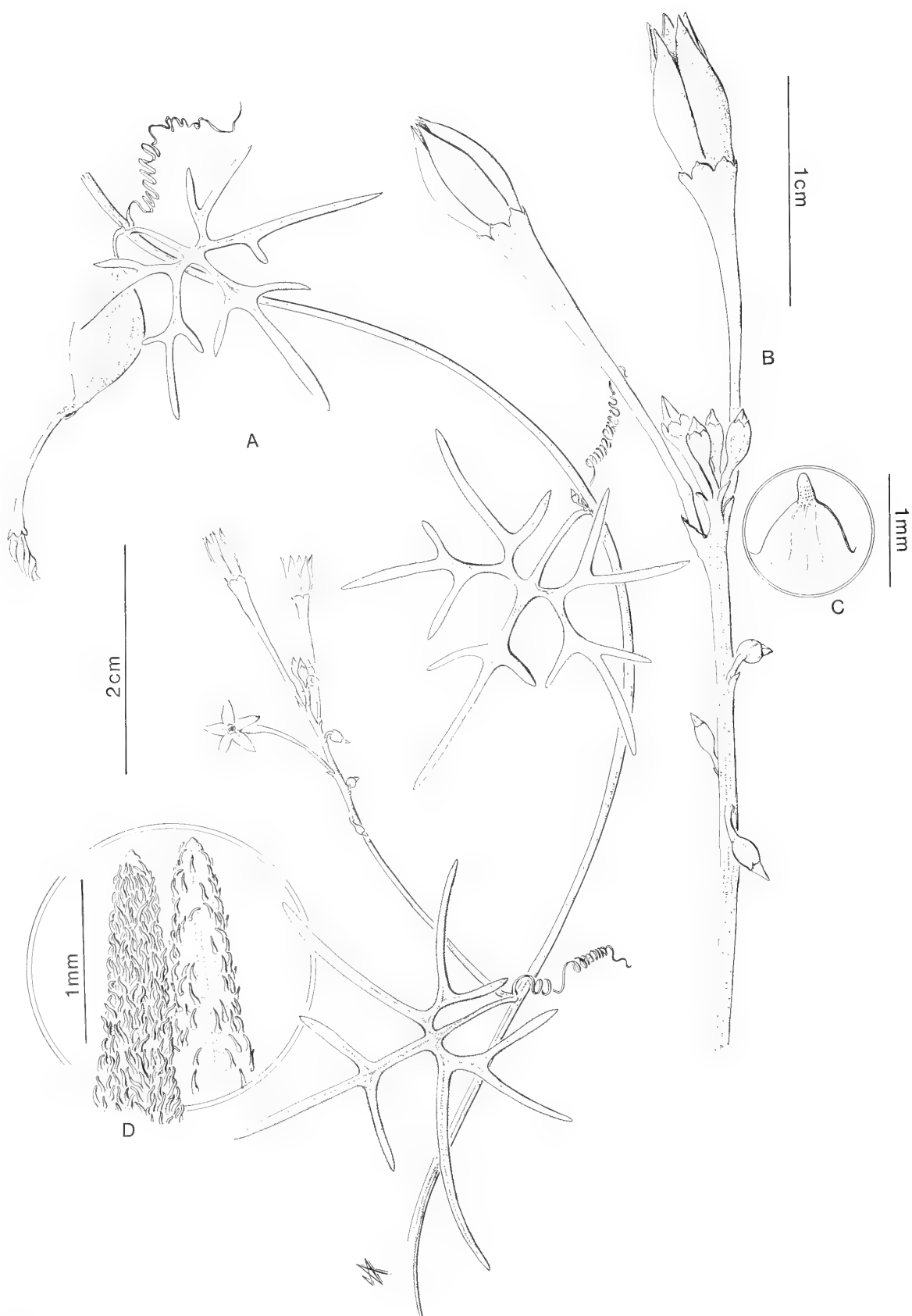
Fig. 3. *Tumamoca mucronata* Kearns. A. flowering and fruiting branch; B. staminate inflorescence; C. sepal showing mucronate apex; D. leaf segment apex showing lower and upper surface pubescence. Drawn from *Johnston, Wendt, & Chiang 11525A* (TEX).

Tumamoca mucronata is known only from the type location in the mountains near the border of Zacatecas and Coahuila in the southern Chihuahuan Desert (Fig. 2). This is an area of shaly-marly limestone and calcareous gravelly soils, interspersed with patches of almost pure gypsum. The species grows in desert scrub with *Larrea tridentata* (DC.) Cov., *Leucophyllum* H. & B., and *Acacia neovernicosa* Isley. The label on the type specimen indicates that the collection is a unicate, which means that there is no opportunity to designate or deposit a type in the Mexican national herbarium (MEXU). Unfortunately, the only specimen known to exist is the type at TEX. An attempt to revisit the type location in July 1991 was unsuccessful due to inclement weather and impassable dirt roads.

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GENETIC FINGERPRINTING OF VARIOUS NATIVE CALIFORNIA CULTIVARS

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Abstract

We employed isozyme and random amplified polymorphic DNA (RAPD) markers to determine the genotypes or "genetic fingerprints" for five groups of cultivars, each of which contain two or more varieties suspected of being identical. Cultivars previously hypothesized to be identical were found to differ isozymically in only one case (*Ceanothus* 'Dark Star' and 'Julia Phelps'). In contrast, only the cultivar pairs *Salvia mellifera* 'Prostrata' and 'Tera Seca' and *Fremontodendron* 'Ken Taylor' (Tree of Life) and 'El Dorado Gold' displayed identical RAPD profiles. Based on these results, we place *Salvia mellifera* 'Prostrata' in synonymy with *Salvia mellifera* 'Tera Seca' because the latter represents the first nomenclaturally valid name for this cultivar. Likewise, *Fremontodendron* 'Ken Taylor' (Tree of Life) has been incorrectly identified and should be treated as synonymous with *Fremontodendron* 'El Dorado Gold'.

Native California cultivars constitute a major portion of the horticultural trade specializing in the propagation and distribution of native plants. Unlike native plants, however, cultivars are produced artificially, being derived from clones, crosses or self-fertilized pure lines. Consequently, the production of new varieties by artificial means requires a system of nomenclature suitable for distinguishing cultivated plants from their wild (native) counterparts. While the rules governing the nomenclature of wild and cultivated plants are basically similar, cultivated plants are treated under separate guidelines set forth in the *International Code of Nomenclature of Cultivated Plants.*

Despite a formal system for naming cultivars, no reliable means of ensuring the stability of cultivar names exists. For example, cultivars are often renamed by various nurseries trading in cultivated plants. Distribution to the public further complicates the problem as cultivated varieties can be transported out of state and reintroduced under a different name. Complications such as these lead to misidentification of cultivars, and confusion regarding their origins.

The purpose of this study is to investigate the identity of five groups of cultivars each of which contains two or more varieties

suspected of being identical. In each case the hypothesis that two or more cultivars are derived from a single clone is based on morphological and phenological observations coupled with insufficient information regarding their origins or the possibility that due to their similarity they have been confused over time in the horticultural trade. The putatively identical varieties include *Heuchera* 'Susanna' and *H.* 'Santa Ana Cardinal' (group 1), *Salvia mellifera* E. Greene 'Little Sur', *S. mellifera* 'Prostrata', and *S. mellifera* 'Tera Seca' (group 2), *Ceanothus* 'Dark Star' and *C.* 'Julia Phelps' (group 3), *Ceanothus* 'Skylark' and *C.* 'Victoria' (group 4) and *Fremontodendron* 'Ken Taylor' (Tree of Life) and *F.* 'El Dorado Gold' (group 5). We also assayed one or more related but genetically distinct individuals for each group to ensure that the techniques we employed provided adequate resolution (hereafter referred to as control genotypes).

In order to distinguish the various cultivars, we employed isozyme and random amplified polymorphic DNA (RAPD) markers (Williams et al. 1990) to determine genotypes for the putatively identical cultivars. Determination of the genotype or "genetic fingerprint" of each cultivar will allow identification of clones. That is, if two or more cultivars exhibit identical genotypes, then the morphology-based hypothesis that they are identical is supported. Alternatively, cultivars which are found to be genotypically dissimilar refute this hypothesis and provide evidence in favor of maintaining their unique cultivar names.

METHODS

Collections. Fresh leaf tissue was collected at Rancho Santa Ana Botanic Garden, Claremont, CA of *Heuchera maxima* E. Greene, *H.* 'Susanna', *H.* 'Santa Ana Cardinal', *Salvia mellifera* 'Point Mugu', *S. mellifera* 'Little Sur', *S. mellifera* 'Prostrata', *S. mellifera* 'Tera Seca,' *Ceanothus impressus* Trel. 'Vandenberg', *C.* 'Dark Star', *C.* 'Julia Phelps', *C. thyrsiflorus* Eschsch. 'Snow Flurry', *C.* 'Skylark', *C.* 'Victoria', *Fremontodendron californicum* (Torrey) Cov. ssp. *decumbens* (R. Lloyd) Munz 'Claremont', *F.* 'Ken Taylor' (Tree of Life), *F.* 'Ken Taylor' (UC Santa Cruz), *F.* 'West Hills Hybrid', *F.* 'El Dorado Gold'.

Enzyme electrophoresis. The following 12 enzymes were analyzed: acid phosphatase (ACPH), aspartate aminotransferase (AAT), glucose-6-phosphate isomerase (GPI), glutamate dehydrogenase (GDH), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucomutase (PGM), phosphogluconate dehydrogenase (PGD), ribulose-bisphosphate carboxylase (RBC), shikimate dehydrogenase (SKD), and triose-phosphate isomerase (TPI).

Electrophoretic procedures generally followed those of Soltis et al. (1983). Leaf tissue was prepared using the Tris-HCl grinding buffer-PVP solution of Soltis et al. (1983). Enzymes were best resolved using the following buffer systems: for TPI, RBC, and AAT, system 6 (Soltis et al. 1983); GPI, GDH, and ME, system 8 (Rieseberg and Soltis 1987); PGD, PGM, and SKD, system 9 (Soltis et al. 1983); and ACPH, MDH, and IDH, system 1 (Soltis et al. 1983).

Genetic interpretation of isozyme phenotypes was based on knowledge of the generally conserved enzyme substructure, compartmentalization, and isozyme number in higher plants (Gottlieb 1981, 1982). Loci were designated sequentially within each group of cultivars, with the most anodally migrating isozyme designated *1*, the next *2*, and so on. Likewise, alleles were designated sequentially, with the most anodally migrating allele designated *a*.

RAPD analysis. For each cultivar, genomic DNA's were isolated from 30 mg of fresh leaf tissue following Rieseberg et al. (1992), which is a modification of the method of Doyle and Doyle (1987). After isolation, the DNA's were further purified with the ELU-QUICK™ DNA Purification Kit (Schleicher & Schuell) and then quantified on a fluorometer.

For analysis of RAPD variation, all 18 DNA's were surveyed for the presence of amplification polymorphisms using 23 arbitrary 10-mer oligonucleotide primers: UBC290 (University of British Columbia Biotechnology Center), A8, A13, A20, B4, B7, B8, B13, B17, B20, C2, C6, C8, C10, C13, C15, C20, D2, D3, D5, D8, D18, D20 (Operon Technologies, Inc.). Primer sequences are given in Fritsch et al. (1993). These primers were chosen for study because they are known to amplify robustly in other flowering plants (Fritsch et al. 1993). Amplification conditions and cycle parameters followed Williams et al. (1990) except that the concentration of *Taq* DNA polymerase was doubled. Amplification products were separated by electrophoresis on 1.5% Tris-borate agarose gels and detected by staining with ethidium bromide.

To eliminate inadvertent scoring of artifactual RAPD variation (Ellsworth et al. 1993; Muralidharan and Wakeland 1993), we varied template and primer concentration by 20–25% in both directions relative to the initial concentration for potentially informative primers (Fig. 1). Only polymorphisms observed under all six different reaction conditions were scored.

RESULTS

Isozymes. Genotypes of all varieties in each group studied are listed for scoreable enzymes and loci in Table 1. Cultivars appearing identical in each group based on morphology are in bold type. Eight or more loci were scoreable for each group, and multiple alleles were
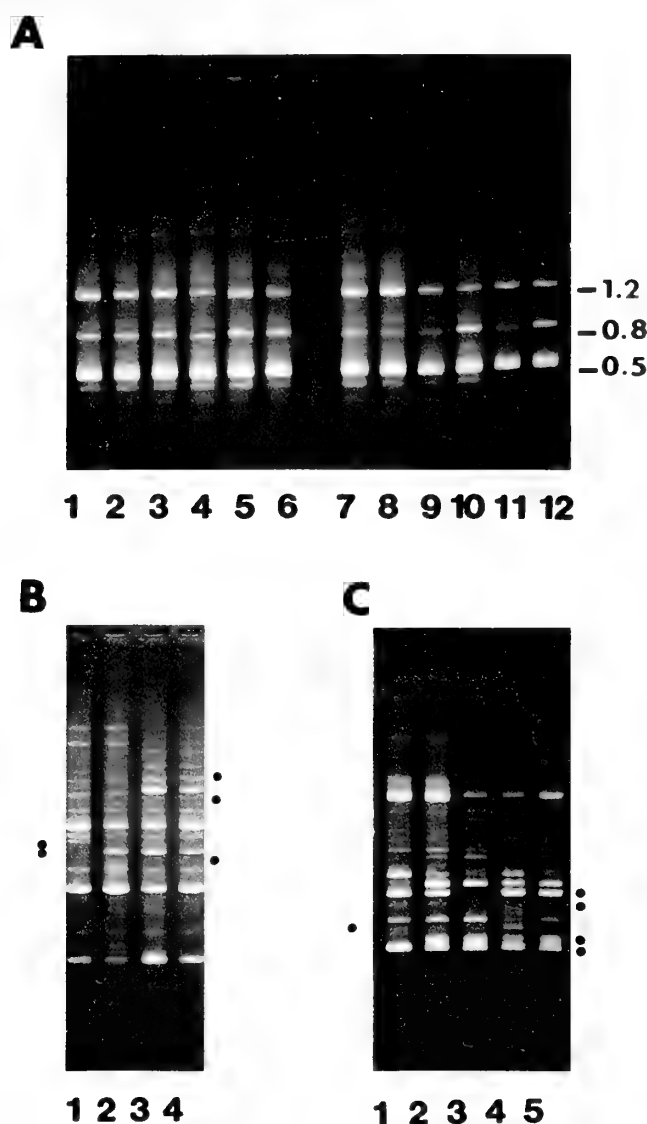
FIG. 1. Photographs of RAPD profiles in several native California cultivars. A) Amplification profiles for primer C13 in *Fremontodendron* 'Ken Taylor' (Tree of Life) (lanes 1–6) and *Fremontodendron* 'El Dorado Gold' (lanes 7–12) with varying concentrations of template and primer: lanes 1 and 7, 20 ng template; lanes 2 and 8, 25 ng template; lanes 3 and 9, 30 ng template; lanes 4 and 10, 0.15 μM primer; lanes 5 and 11, 0.2 μM primer; lanes 6 and 12, 0.25 μM primer. Fragment sizes in kb are given to the right of the photograph. Note relative constancy of RAPD profiles. B) Amplification profiles for primer A8 in the *Salvia* cultivar group: lane 1, *Salvia mellifera* 'Point Mugu'; lane 2, *S. mellifera* 'Little Sur'; lane 3, *S. mellifera* 'Prostrata'; and lane 4, *S. mellifera* 'Tera Seca'. Black dots adjacent to photograph indicate informative fragments. Sizes of informative fragments are in descending order: 2.1, 1.7, 0.95, 0.92, and 0.85 kb. C) Amplification profiles for primer B7 in the *Fremontodendron* group: lane 1, *F. californicum* ssp. *decumbens* 'Claremont'; lane 2, *F.* 'Ken Taylor' (Tree of Life); lane 3, *F.* 'Ken Taylor' (UC Santa Cruz); lane 4, *F.* 'West Hills Hybrid'; and lane 5, *F.* 'El Dorado Gold'. Black dots adjacent to photograph indicate informative fragments. Sizes of informative fragments are in descending order: 0.8, 0.75, 0.60, 0.55, and 0.50 kb.

TABLE 1. ISOZYME DATA FOR SELECTED CALIFORNIA CULTIVARS. Morphologically indistinguishable cultivars in each group are in bold. Control genotypes are marked with an asterisk.

Taxon	Cultivar	Locus/geno-type	
		Aat1	*Aat2*
*Heuchera maxima	#15,595	*aa*	*aa*
Heuchera	**'Susanna'**	*aa*	*aa*
Heuchera	**'Santa Ana Cardinal'**	*aa*	*aa*
*Salvia mellifera	'Point Mugu'	*aa*	*aa*
S. mellifera	**'Little Sur'**	*aa*	*aa*
S. mellifera	**'Prostrata'**	*aa*	*aa*
S. mellifera	**'Tera Seca'**	*aa*	*aa*
*Ceanothus impressus	'Vandenberg'	—	—
Ceanothus	**'Dark Star'**	—	—
Ceanothus	**'Julia Phelps'**	—	—
*Ceanothus thyrsiflorus	'Snow Flurry'	—	—
Ceanothus	**'Skylark'**	—	—
Ceanothus	**'Victoria'**	—	—
*Fremontodendron californicum ssp. *decumbens*	'Claremont'	—	—
Fremontodendron	**'Ken Taylor' (Tree of Life)**	—	—
*Fremontodendron	'Ken Taylor' (UC Santa Cruz)	—	—
*Fremontodendron	'West Hills Hybrid'	—	—
Fremontodendron	**'El Dorado Gold'**	—	—

found for at least two loci in each group. Cultivars previously hypothesized to be identical were found to differ isozymically in only one case (*Ceanothus* 'Dark Star' and 'Julia Phelps'). Although most cultivars differed by at least one polymorphism from the control genotype for their group, this was not the case for all members of the *Fremontodendron* group.

RAPD's. Much higher levels of polymorphism were observed for the RAPD amplification profiles. The control genotypes for each group differed from the cultivars by numerous reproducible markers. Likewise, several of the cultivars hypothesized to represent clones differed with respect to numerous RAPD polymorphisms (Table 2), including *Heuchera* 'Susana' and *H.* 'Santa Ana Cardinal' which differed by 22 polymorphisms, *Ceanothus* 'Dark Star' and *C.* 'Julia Phelps' which differed by 13 polymorphisms, and *Ceanothus* 'Skylark' and *C.* 'Victoria' which differed by 14 polymorphisms. In addition, *Salvia mellifera* 'Little Sur' differed from the other two *S. mellifera* cultivars by six polymorphisms (Table 2). In contrast, *Fre-*

TABLE 1. CONTINUED.

Locus/genotype												
Aat3	*Gpi1*	*Gpi2*	*Idh*	*Mdh1*	*Me*	*Pgd1*	*Pgd2*	*Pgm1*	*Pgm2*	*Rbc*	*Tpi1*	*Tpi2*
—	—	—	*aa*	*aa*	—	—	—	*bb*	*aa*	—	*aa*	*aa*
—	—	—	*aa*	*aa*	—	—	—	*aa*	*aa*	—	*ab*	*aa*
—	—	—	*aa*	*aa*	—	—	—	*aa*	*aa*	—	*ab*	*aa*
aa	*aa*	*ab*	—	*aa*	*aa*	—	—	—	—	*aa*	*ab*	*ab*
aa	*aa*	*bb*	—	*aa*	*aa*	—	—	—	—	*aa*	*ab*	*ab*
aa	*aa*	*bb*	—	*aa*	*aa*	—	—	—	—	*aa*	*ab*	*ab*
aa	*aa*	*bb*	—	*aa*	*aa*	—	—	—	—	*aa*	*ab*	*ab*
—	*aa*	*bb*	—	*aa*	—	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*
—	*aa*	*bb*	—	*aa*	—	*aa*	*aa*	*aa*	*ab*	*aa*	*ab*	*aa*
—	*aa*	*ab*	—	*aa*	—	*aa*	*aa*	*aa*	*ab*	*aa*	*ab*	*aa*
—	*aa*	*aa*	*aa*	*aa*	—	*ab*	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*
—	*aa*	*aa*	*ab*	*aa*	—	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*
—	*aa*	*aa*	*ab*	*aa*	—	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*
—	*aa*	*aa*	*ab*	*aa*	—	—	—	*aa*	—	*aa*	*ac*	*aa*
—	*aa*	*aa*	*ab*	*aa*	—	—	—	*aa*	—	*aa*	*ac*	*aa*
—	*aa*	*aa*	*ab*	*aa*	—	—	—	*aa*	—	*aa*	*ab*	*aa*
—	*aa*	*aa*	*ab*	*aa*	—	—	—	*aa*	—	*aa*	*ab*	*aa*
—	*aa*	*aa*	*ab*	*aa*	—	—	—	*aa*	—	*aa*	*ac*	*aa*

montodendron 'Ken Taylor' (Tree of Life) and *F.* 'El Dorado Gold' were identical with respect to their RAPD profiles (Fig. 1) as were *Salvia mellifera* 'Prostrata' and 'Tera Seca' (Fig. 1; Table 2).

DISCUSSION

This study demonstrates the utility of isozymes and RAPD's for "genetic fingerprinting" plant cultivars suspected to be part of a single clone. Since many plants of horticultural importance are propagated asexually, all individuals of a cultivar are likely to belong to a single genet. All individuals in that genet will then be expected to yield identical isozyme and RAPD patterns. For example, the *Heuchera, Fremontodendron,* and *Ceanothus* cultivars analyzed herein are of hybrid origin and are by necessity propagated asexually primarily from cuttings (the *Heuchera* clones have been produced by tissue culture as well) to maintain their inherent unique characteristics. The *Salvia mellifera* clones are all prostrate forms which have been solely propagated from cuttings.

TABLE 2. RAPD DATA FOR SELECTED CALIFORNIA CULTIVARS. Morphologically indistinguishable cultivars in each group are in bold. Only data from reproducible and informative polymorphisms are given. Control genotypes are marked with an asterisk. The presence or absence of fragments is indicated by a "+" and "—", respectively.

Taxon: *Heuchera maxima*

Cultivar	UBC290			B17						C2				C8								C13						
Fragment (kb):	1.5	1.1	0.8	1.5	0.90	0.85	0.70	0.40	1.4	0.70	0.65	0.55	0.51	1.35	1.3	1.0	0.9	0.8	0.7	0.5	0.4	1.5	1.1	0.76	0.68	0.66	0.6	0.45
*Heuchera maxima #15,595	−	+	−	+	−	−	+	+	−	+	+	−	−	+	−	−	−	−	+	−	−	−	−	−	−	−	−	+
Heuchera 'Susanna'	+	−	+	−	+	+	+	−	+	−	+	+	+	−	+	−	+	+	−	+	−	+	−	+	−	−	+	−
Heuchera 'Santa Ana Cardinal'	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	−	−	−	+	−	+	−	+	+	−	+

Taxon: *Salvia mellifera*

Cultivar	A8					A20				B4		B8		C2			C8	C10			C13	C15	D2		D3	D8	D18		
Fragment (kb):	2.1	1.7	0.95	0.92	0.85	1.4	1.1	0.9	0.7	0.90	0.45	1.1	0.65	1.4	0.55	0.50	0.22	2.1	1.2	1.1	0.75	1.8	0.7	0.67	0.8	0.75	1.4	1.25	1.0
*Salvia mellifera 'Point Mugu'	−	−	+	−	+	−	+	+	+	+	−	−	+	+	+	+	−	−	+	+	−	+	+	+	−	−	+	−	−
S. mellifera 'Little Sur'	−	−	−	+	−	+	+	+	−	−	+	+	−	−	−	+	+	+	−	−	+	−	+	−	+	−	−	+	+
S. mellifera 'Prostrata'	+	+	−	+	−	+	+	+	+	+	−	+	−	+	+	−	+	+	+	+	+	−	−	+	+	+	+	−	+
S. mellifera 'Tera Seca'	+	+	−	+	−	+	−	+	+	+	+	−	−	+	−	+	+	−	+	+	+	−	+	+	+	+	+	−	+

Taxon: *Ceanothus impressus*

Cultivar	A8				A20					B4	B7					C2			C6	C13		D3	D5	D8		
Fragment (kb):	1.8	1.6	1.0	0.52	1.7	1.6	0.90	0.62	0.42	1.7	0.8	0.78	0.6	0.5	0.4	1.4	0.75	0.72	0.4	0.8	0.5	0.8	1.0	0.85	0.52	
*Ceanothus impressus 'Vandenberg'	+	+	+	+	+	+	−	−	−	−	−	−	+	+	+	−	−	−	+	+	+	−	+	−	+	
Ceanothus 'Dark Star'	−	−	+	−	+	−	+	+	+	+	+	+	+	+	−	+	+	−	+	−	+	+	+	+	+	
Ceanothus 'Julia Phelps'	−	−	−	+	+	−	+	+	+	+	−	−	−	−	+	−	+	+	−	+	−	+	+	+	−	

Taxon: *Ceanothus thyrsiflorus*

Cultivar	A13	A20			B8			B17		C2			C6				C20			D3
Fragment (kb):	0.52	1.1	0.85	0.52	1.2	0.90	0.80	0.6	0.55	0.9	0.85	0.8	0.7	0.65	0.5	0.4	1.4	0.8	0.6	0.46
*Ceanothus thyrsiflorus 'Snow Flurry'	−	−	+	+	−	+	−	+	+	+	+	+	+	+	+	−	+	−	+	+
Ceanothus 'Skylark'	+	+	+	−	+	+	−	+	+	+	−	−	+	+	−	+	+	+	−	−
Ceanothus 'Victoria'	+	+	−	+	−	−	+	+	+	−	+	−	−	−	+	+	−	+	+	−

Taxon: *Fremontodendron californicum ssp. decumbens*

Cultivar	A8		A20		B7					B8			B17		B20	C8	D3
Fragment (kb):	1.4	0.3	1.2	1.0	0.8	0.75	0.60	0.55	0.5	1.0	0.9	0.78	1.0	0.8	1.0	0.78	0.7
*Fremontodendron californicum ssp. decumbens 'Claremont'	−	+	+	−	−	+	+	+	+	−	−	−	−	−	−	−	−
Fremontodendron 'Ken Taylor' (Tree of Life)	−	+	+	−	+	+	+	+	−	−	+	−	−	+	−	+	+
*Fremontodendron 'Ken Taylor' (UC Santa Cruz)	+	−	−	+	+	+	+	−	+	+	−	+	+	+	−	+	+
*Fremontodendron 'West Hills Hybrid'	+	−	−	+	+	+	−	+	+	+	+	+	−	+	+	−	−
Fremontodendron 'El Dorado Gold'	−	+	+	−	+	+	+	+	+	−	+	−	−	+	−	+	−

To date, cultivar identification has been accomplished primarily with isozyme and morphological polymorphisms (e.g., Tanksley and Orton 1983; Granger 1993). However, these descriptors sometimes are not variable enough to distinguish individual genotypes. For example, *Heuchera* 'Susana' and *H.* 'Santa Ana Cardinal', *Ceanothus* 'Skylark' and *C.* 'Victoria', and *Salvia mellifera* 'Little Sur' and the other two *S. mellifera* cultivars were identical in terms of morphology and isozymes, but could be easily distinguished based on their RAPD amplification profiles. Nonetheless, these results should not be used to denigrate the utility of isozymes and morphology for cultivar identification and discrimination. Both types of data can be gathered more efficiently and with less expense than RAPD data. Furthermore, artifactual variation is much less of a problem for isozymes than RAPD's, although the opposite is true for morphological data. Moreover, if cultivars can be shown to differ isozymically or morphologically, the need for time-consuming and expensive DNA fingerprinting studies is eliminated. Only where cultivars cannot be discriminated with isozymes or morphology are more detailed genetic tests required to verify the hypothesis of clonal identity.

The three *Salvia mellifera* cultivars are prostrate forms from Monterey County, however two appear to represent identical clones while 'Little Sur' is genetically distinct. Likewise, *Fremontodendron* 'Ken Taylor' (Tree of Life), 'Ken Taylor' (UC Santa Cruz), 'West Hills Hybrid', and 'El Dorado Gold' all are supposed to represent F_1 progeny of *Fremontodendron californicum* ssp. *decumbens* × *Fremontodendron* 'California Glory'. However, 'Ken Taylor' (Tree of Life) and 'El Dorado Gold' are morphologically identical, whereas the other two siblings are quite distinctive. Thus, the genetic data confirming the clonal nature of the former was anticipated.

What was more surprising was the fact that the *Heuchera* and both *Ceanothus* cultivar pairs are clearly different genetically. Both *Heuchera* 'Susana' and *H.* 'Santa Ana Cardinal' are believed to be clonally propagated F_1 hybrids of *H. maxima* × *H. sanguinea*. Given their distinctive RAPD profiles, however, it is likely that the cultivars are derived from two independent matings between these two species. Both pairs of morphologically similar, clonally propagated, hybrid *Ceanothus* cultivars also appear to represent independent crosses between their hypothesized parental species (*Ceanothus impressus* × *C. papillosus* Torrey & A. Gray var. *roweanus* McMinn ⇒ 'Dark Star' and 'Julia Phelps' and *C. thyrsiflorus* × *C. velutinus* Hook ⇒ 'Skylark' and Victoria').

Based on these results, separate cultivar names for *Salvia mellifera* 'Prostrata' and 'Tera Seca' and *Fremontodendron* 'Ken Taylor' (Tree of Life) and 'El Dorado Gold' should not be maintained. Thus, we place *Salvia mellifera* 'Prostrata' in synonymy with *S. mellifera* 'Tera

Seca' because the latter represents the first nomenclaturally valid name for this cultivar. Likewise, *Fremontodendron* 'Ken Taylor' (Tree of Life) has been incorrectly identified and should be treated as synonymous with *Fremontodendron* 'El Dorado Gold'.

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COAST LIVE OAK (*QUERCUS AGRIFOLIA*) EFFECTS ON GRASSLAND BIOMASS AND DIVERSITY

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Abstract

Spatial variation in environmental conditions and herbaceous community structure was studied across the ecotone between coast live oak (*Quercus agrifolia*) woodland and grassland in northern California. Oak canopy reduced light incidence (2.8% compared to open) but increased soil moisture and nitrogen availability underneath. The understory herbaceous layer had a different species composition from open grassland, lower species richness, lower above-ground biomass, a delayed seasonal growth, and different biomass partitioning by species. Grassland diversity and biomass fitted a second order polynomial regression, with maximum at 570 gm^{-2}, and reduced diversity in the harsh, shaded, low-productivity understory. The heterogeneity of physical conditions induced by oak canopy maintains a higher landscape (gamma) diversity of herbaceous plants.

Coast live oak (*Quercus agrifolia*) woodlands extend along the coastal hills and plains of California, from San Diego to Mendocino County, covering about 3350 km² (Griffin and Critchfield 1972; Bolsinger 1988). The oak woodland intersperses frequently with open grassland, forming a landscape mosaic.

The dominant evergreen coast live oak trees change environmental conditions in the understory, in terms of reduced light, less extreme temperatures, altered water availability and evapotranspiration, and soil enriched in nutrients and organic matter (Parker and Muller 1982). Grassland species composition and production consequently differ considerably under canopy compared to open.

We have previously reported differences in soil seed bank and seedling establishment patterns between open grassland and coast live oak understory in northern California (Marañón and Bartolome 1989). In this paper we document community-level grassland changes along the ecotone between coast live oak (*Quercus agrifolia*) woodland and open grassland, in the same study area. Features of the community structure studied were species composition, above-ground biomass and its seasonal partitioning among species, and species richness. We show how tree canopy influences plant diversity

in this evergreen oak-dominated landscape. Small-scale changes in understory diversity should be important for maintaining biological diversity in managed landscapes.

Methods

Study site. The study was located at the University of California's Russell Reservation, about 20 km inland from San Francisco Bay, in the Coast Range. The climate is of mediterranean-type, with cool, humid winters and warm, dry summers. Annual precipitation averaged 1080 mm in 1982–1983, and 520 mm in 1983–1984, whereas the average annual rainfall (14 years) was 680 mm. Mean annual temperature was 14°C with a maximum monthly mean of 28°C in July and a minimum monthly mean of 5°C in December.

Sandstone hills are overlaid by a loamy, inceptisol (Millsholm series) soil. A South-facing 20° slope covered by annual grassland and bounded on East and West by coast live oak (*Quercus agrifolia*) woodland was selected as the study area. The oak canopy cover was over 90% with average density of 170 trees ha^{-1} and average dbh of 46 cm. On the reservation, no grazing by livestock has been allowed for the last 20 years, but impact by deer, voles and gophers may be locally important (Marañón and Bartolome 1989).

Sampling. Four transects were located across the oak woodland–open grassland ecotone, two on the east and two on the west boundaries of a grassland. Five 1 × 1 m plots were located along each transect, one representing the oak understory (1–3 m from the trunk and more than 7 m inside from the oak canopy edge), one in the open grassland (more than 5 m outside from the canopy edge) and three at the canopy edge (where more spatial variation is expected). In each plot, a square of 25 × 25 cm was located randomly and the aboveground biomass inside was clipped. The operation was repeated (excluding previous clipping sites) eight times during the growing season 1983–1984. The clipped biomass was sorted by species, oven-dried at 65°C and weighed.

Ten plots of 25 × 25 cm were randomly located in each of three defined habitats: oak understory, oak canopy edge and open grassland. Aboveground biomass was clipped on May 1983, separated into dead (mulch) and live plant materials, oven-dried at least 24 hours at 65°C and weighed.

Environmental conditions. Light incidence at the herbaceous level was measured at noon in July (five measurements on each plot), using a LI-COR Quantum Sensor.

Soil moisture was measured using the gravimetric method. The weight loss of 10 cm depth soil cores was recorded after 24 hours
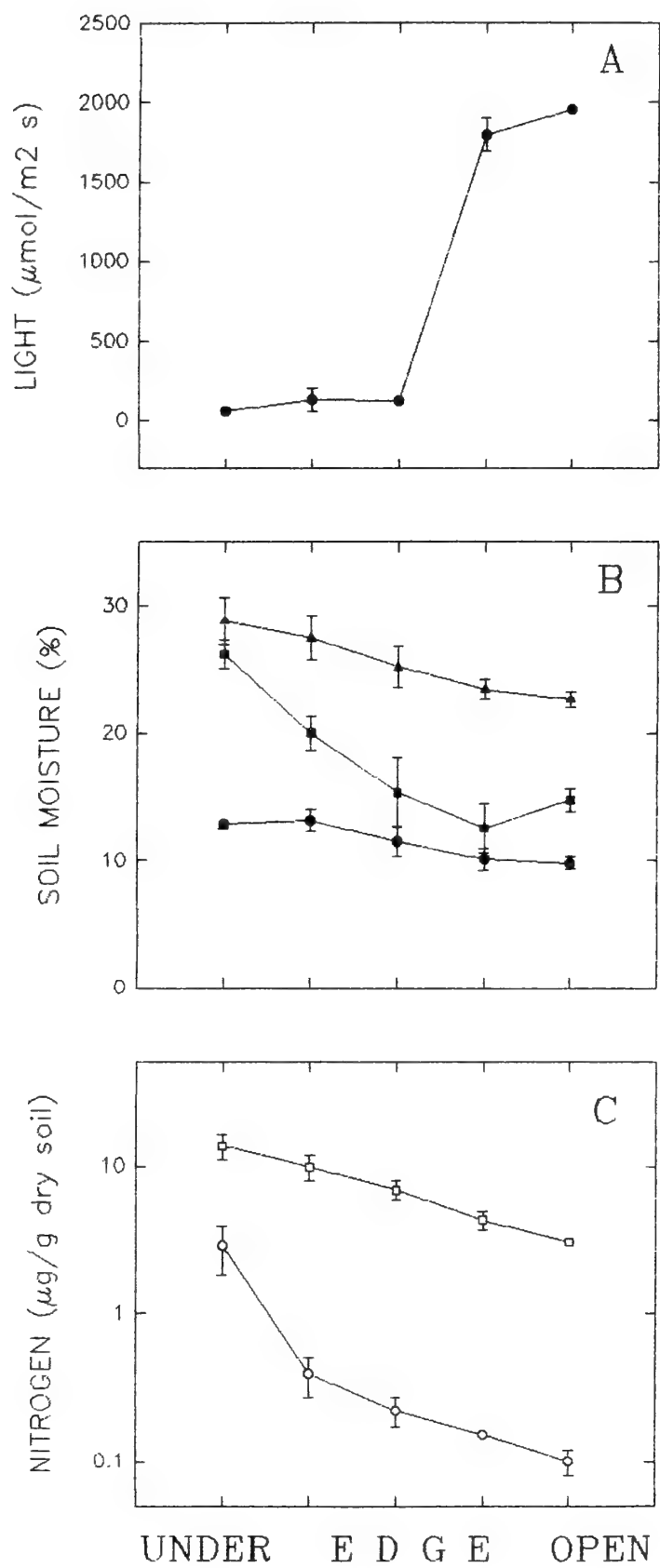
FIG. 1.   Environmental variables along the ecotone between oak understory and open grassland (mean and standard error bar). A: Light incidence at noon July 30 (n = 15); B: Soil moisture (n = 4) in October 18 (●), December 12 (▲) and March 30 (■); C: Nitrogen content in top soil (n = 4), as nitrate (○) and ammonium (□).

oven-drying at 105°C. Soil moisture measurements were made in October and December 1983, and in March 1984.

Inorganic nitrogen, as nitrate and ammonium, in top soil samples from March 1984 was determined in KCl extracts colorimetrically (Jackson et al. 1988).

Numerical analysis. Species composition and abundance of twenty (5 plots from 4 transects) aboveground biomass samples from May 1984 were analyzed with detrended correspondence analysis (DCA) using a CANOCO program and selecting the following options: de-trending by 2nd order polynomial, logarithmic transformation of the biomass data, exclusion of infrequent species ($F = 1$), and down-weighting of rare species (Ter Braak 1988).

Grassland peak aboveground biomass and species richness, as well as environmental variables were averaged among the four transects to obtain a general spatial trend along the oak understory-open grass-land ecotone. Cumulative species richness along the transect was calculated to reflect landscape (gamma) diversity.

The relationship between peak aboveground biomass and species richness was studied using both the 30 random samples from 1983 and the 20 plot samples from 1984 (total of 50 samples). A second order polynomial regression was fitted and the biomass for maxi-mum diversity (BMD) was calculated as the curve's maximum (Gar-cía et al. 1993).

Species nomenclature follows Munz (1968).

Results

Environmental conditions. July mid-day light incidence at the herbaceous level under the evergreen oak canopy averaged 53.8 μmol m^{-2} sec^{-1}, although sunfleck measurements reached 139 μmol m^{-2} sec^{-1}. At the oak canopy edge the average incident radiation in-creased to 125–130 μmol m^{-2} sec^{-1} and just outside the canopy projection the light sharply increased to 1794.7 μmol m^{-2} sec^{-1} (about 14 times) in the zone with shading during early and late daytime period. The average full sun radiation recorded in open grassland was 1950.7 μmol m^{-2} sec^{-1} (Fig. 1A).

Soil moisture at the beginning of the rainy season (October 18) was relatively low (9.8–12.9%) along the transect. Two months later (December 12) the top soil was moist (22.7–28.8%) all along the transect. On both dates, the oak understory soil was slightly moister than open grassland soil. Major changes of top soil moisture were observed during early spring (March 30), at the time of rapid plant growth, when open grassland soil suffered a more rapid water loss than understory soil (Fig. 1B).

Nitrogen content of the top soil, either as nitrate or ammonium,
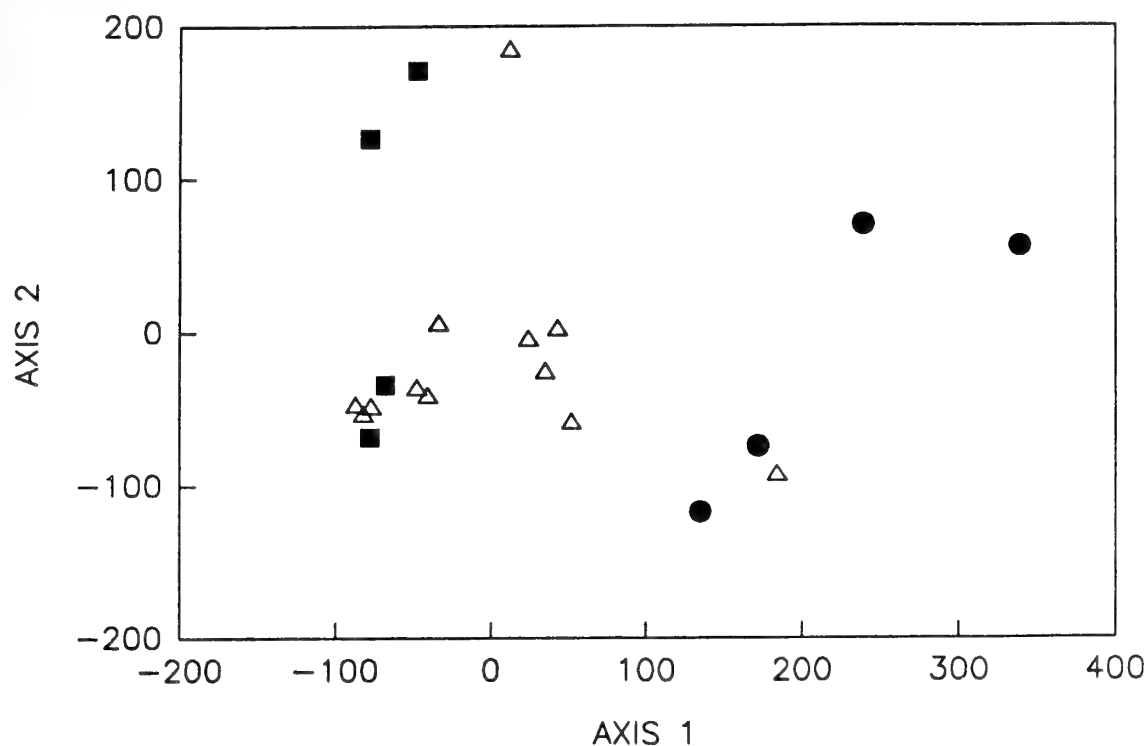
FIG. 2.   DCA analysis of aboveground biomass samples from the oak understory
(●), canopy edge (△) and open grassland (■).

showed a decrease along the transect, from the oak understory to-
wards the open grassland (Fig. 1C). Mean nitrate content, in March,
near the oak trunk was 2.9 μg g^{-1} dry soil, decreasing at the oak
canopy edge (0.15–0.39 μg g^{-1} dry soil) and the minimum value was
recorded in the open grassland soil (0.10 μg g^{-1} dry soil). Ammonium
content in top soil decreased more slowly from the inner oak un-
derstory (13.62 μg g^{-1} dry soil) towards the oak canopy edge (4.32–
9.86 μg g^{-1} dry soil), and the minimum value was in the open
grassland soil (3.07 μg g^{-1} dry soil).

Species composition. DCA analysis of 26 species biomass in 20
samples clearly separated oak understory samples (at the right ex-
treme of axis 1) from open grassland samples (at the left extreme of
axis 1), whereas canopy edge samples are dispersed in-between and
tend to be closer to the open grassland samples (Fig. 2). *Stellaria
media, Galium aparine, Montia perfoliata* and *Carduus pycnocepha-
lus* are among the species with higher positive scores for axis 1,
differentiating the oak understory samples. *Bromus mollis, Gera-
nium dissectum, Vicia sativa* and *Lupinus bicolor* show high negative
scores for axis 1, and they are characteristic of open grassland sam-
ples.

Peak aboveground biomass. The average aboveground biomass in
the oak understory, near the tree trunk (128.9 g m^{-2}) increased

almost three times at the canopy edge (359.8 g m^{-2}), with a similar value to the open grassland (365.7 g m^{-2}) (Fig. 3A).

Seasonal biomass. The fastest increase of biomass in the open grassland occurred between February and April, and by June most of the plants were dried up. In the oak understory, the growth was slower than in the open but the decline was retarded, some plants remaining green until July (Fig. 4). The canopy edge samples showed a similar growth pattern to the open grassland samples but the decline at the end of the cycle was delayed, e.g., June aboveground biomass accounted for 90.8 g m^{-2} at the oak canopy edge and 12.1 g m^{-2} in the open.

Biomass partitioning by species. In the oak understory, *Montia perfoliata, Stellaria media* and *Galium aparine* made up 56% of the aboveground biomass early in the growing season (February), declining as a proportion of the community biomass in spring. *Carduus pycnocephalus,* with slower growth, was the dominant species later in the growing season, and some plants survived until July. *Bromus diandrus* and *Lolium multiflorum* were the most abundant annual grasses throughout the growing season. No annual legumes were recorded in the transect understory samples (Fig. 5A), although the perennial *Lathyrus vestitus* was present in a few (30%) of the random samples.

Typical understory species like *Montia perfoliata, Stellaria media* and *Galium aparine* only summed up to 3.8% of the aboveground biomass at the oak canopy edge. *Carduus pycnocephalus* (9%) and *Bromus diandrus* (12.2%) showed a significant biomass contribution in May samples. *Lolium multiflorum* was the dominant species (49.6%) in the spring community biomass. Other annual grasses, like *Bromus mollis* and *Avena fatua,* as well as annual legumes like *Medicago polymorpha* and *Vicia sativa* had a minor biomass contribution. Perennial *Elymus triticoides* and *Aster chilensis* increased their biomass proportion later in the growing season (Fig. 5B).

Four annual grasses, *Bromus diandrus, Lolium multiflorum, Avena fatua* and *Bromus mollis* made up 88.1% of the spring aboveground biomass in the open grassland. *Carduus pycnocephalus* represented 12.9% of the biomass in the April samples. A few annual legumes, *Lupinus bicolor, Vicia sativa* and *Medicago polymorpha* summed up to 14.5% of the community biomass in May. Other important species, in term of biomass, were *Hypochoeris glabra, Geranium dissectum* and later in the growing season, the perennial *Elymus triticoides* (the only living biomass in July samples) (Fig. 5C).

Species richness. Species density was lower near the oak trunk (average of 5.8 species 0.0625 m^{-2}) than at the oak canopy edge or
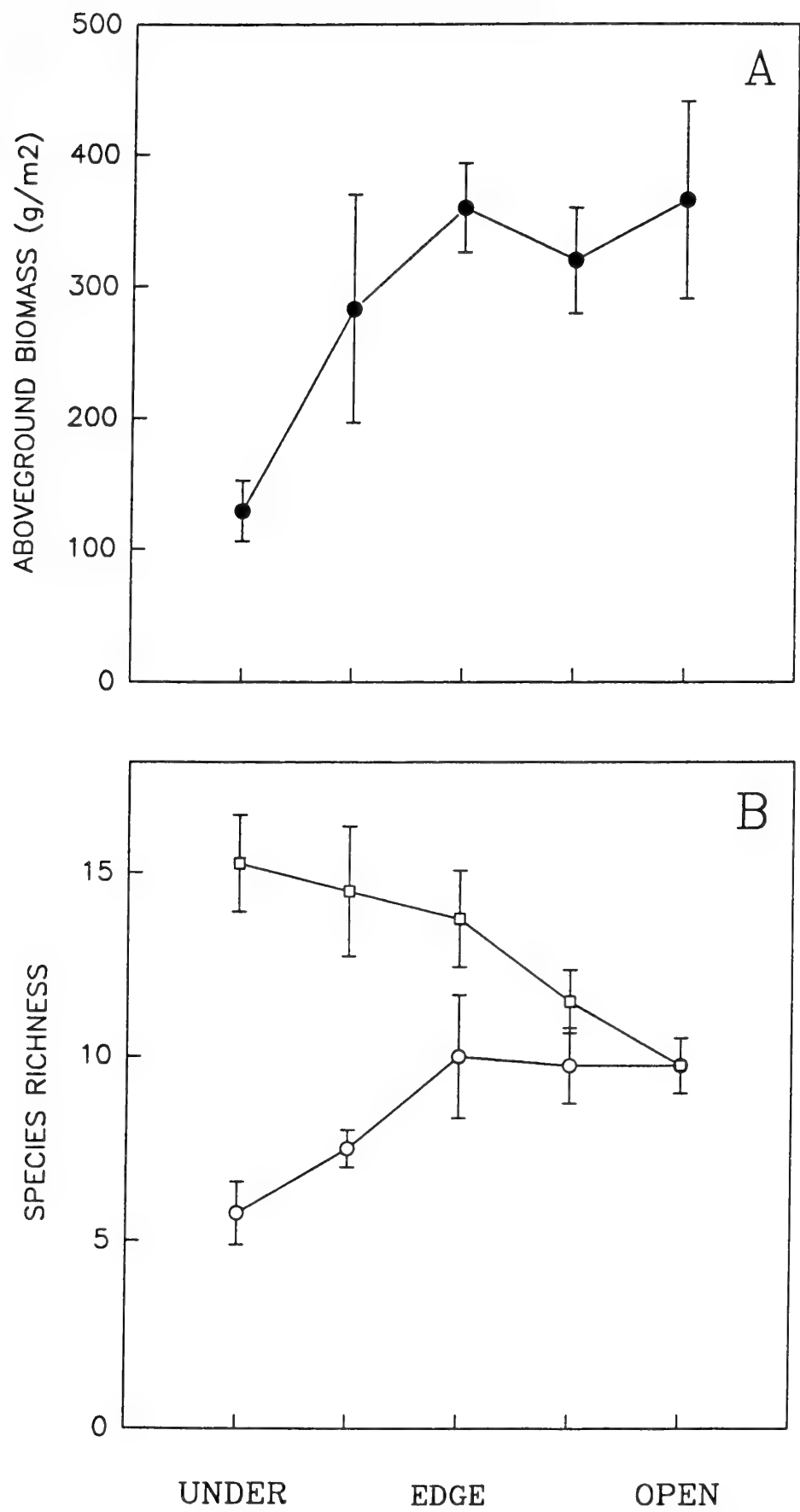
FIG. 3.   Aboveground biomass (A), species richness (B, circle) and cumulative species richness (B, square) along the ecotone between the oak understory and open grassland (mean and standard error bar).
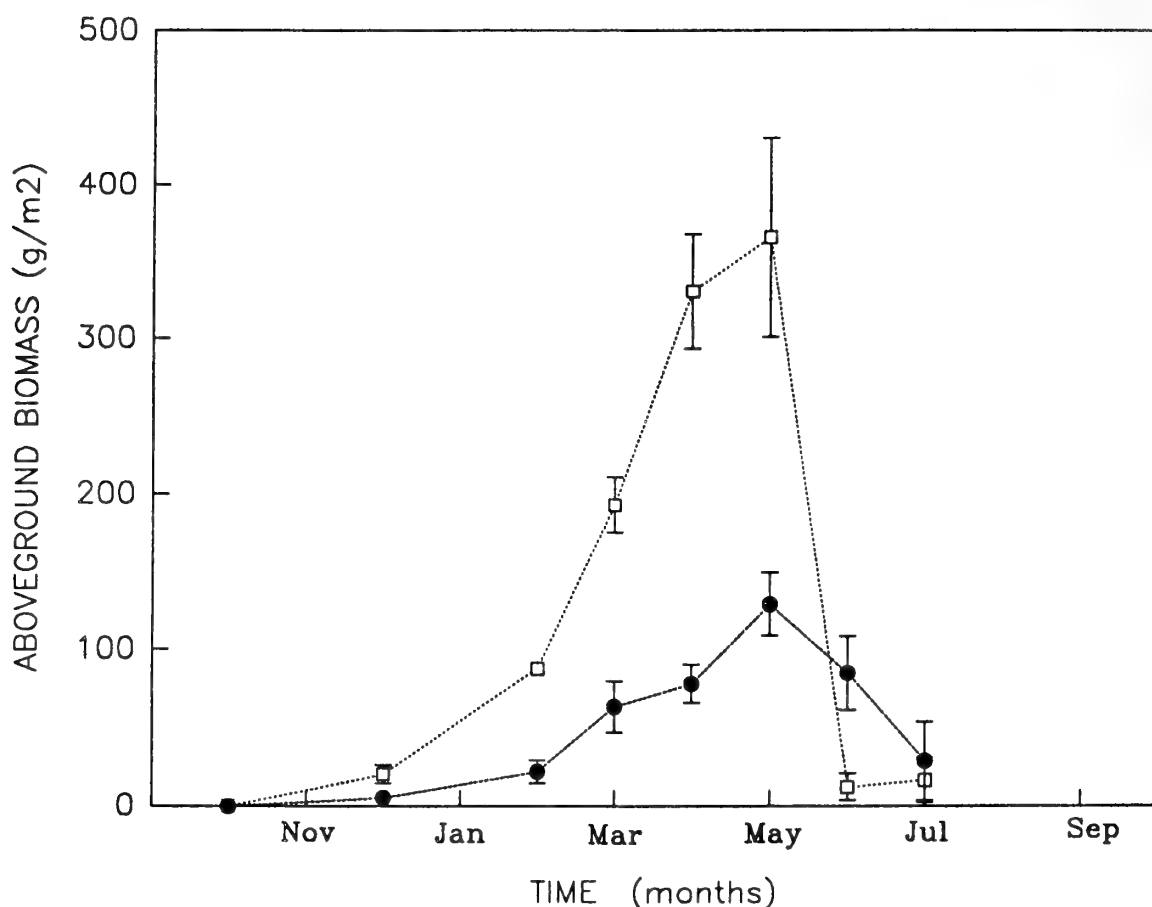
Fig. 4.   Monthly aboveground biomass (mean and standard error bar, n = 4) in the oak understory (●) and open grassland (□).

in the open grassland (averages of 7.5–10.0 and 9.8 species 0.0625 m^{-2} respectively) (Fig. 3B). Cumulative species richness along the transect, plotted from the open grassland towards the understory (Fig. 3B), increased up to an average of 15.3 species recorded per transect.

Biomass and diversity. The relationship between aboveground biomass and species richness fitted a second order polynomial regression (r = 0.49, F = 7.47, P = 0.009) (Fig. 6). The calculated maximum for the function (BMD value) was 570.12 g m^{-2}. Oak understory samples showed lower aboveground biomass and species richness than oak canopy edge and open grassland samples.

DISCUSSION

The evergreen oak canopy changes the physical and chemical environment for the herbaceous plants in the understory. Three main factors affecting plant distribution and abundance are light, soil moisture and nitrogen availability. The sharp reduction of light incidence (2.8% of open conditions) precludes seedling establishment
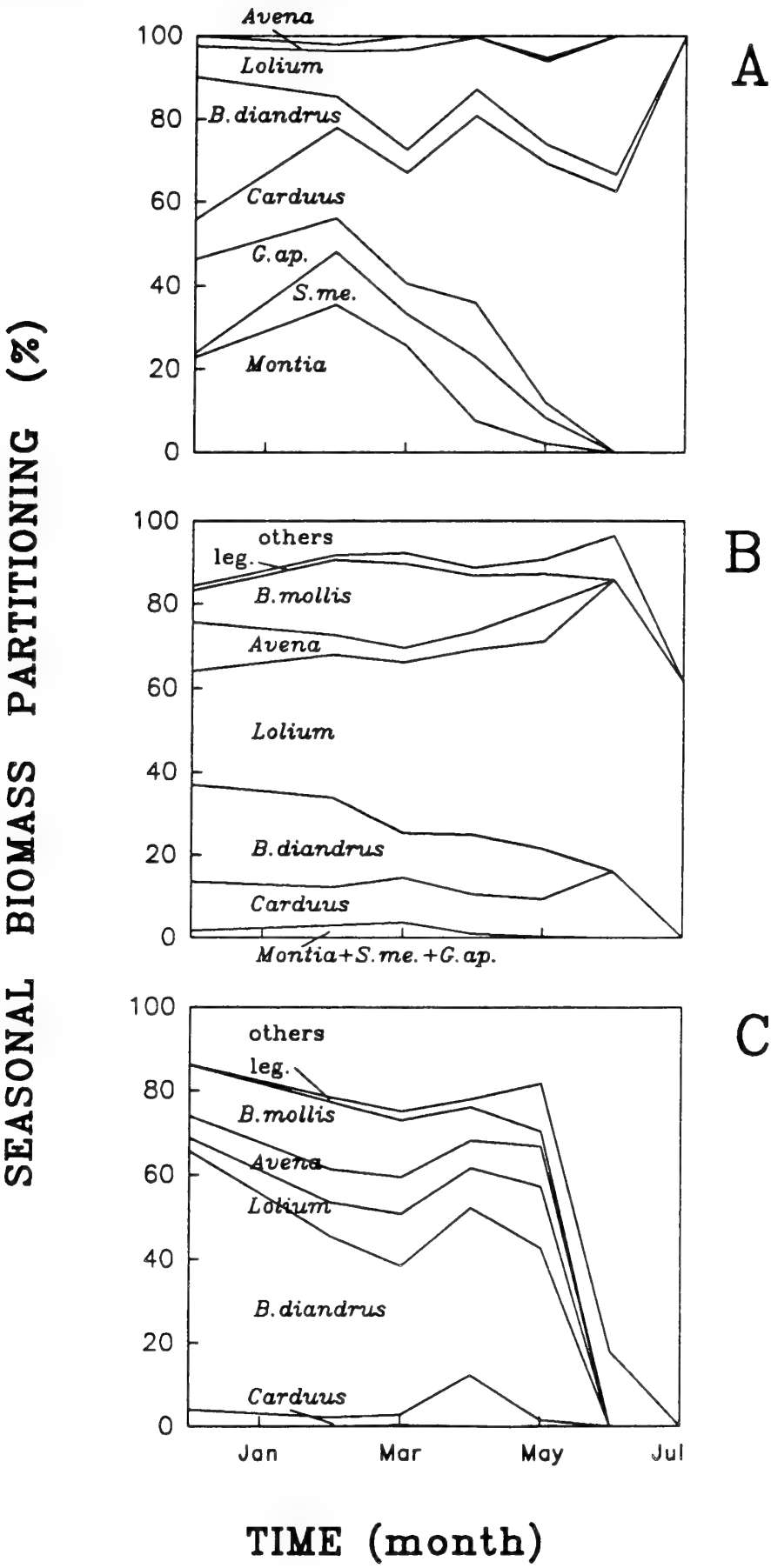
FIG. 5. Percent composition of the seasonal aboveground biomass in the oak understory (A), canopy edge (B) and open grassland (C). Species are named by genus or species (*Bromus*), except abbreviated G.ap. = *Galium aparine* and S.me. = *Stellaria media*, and leg. = legume species.
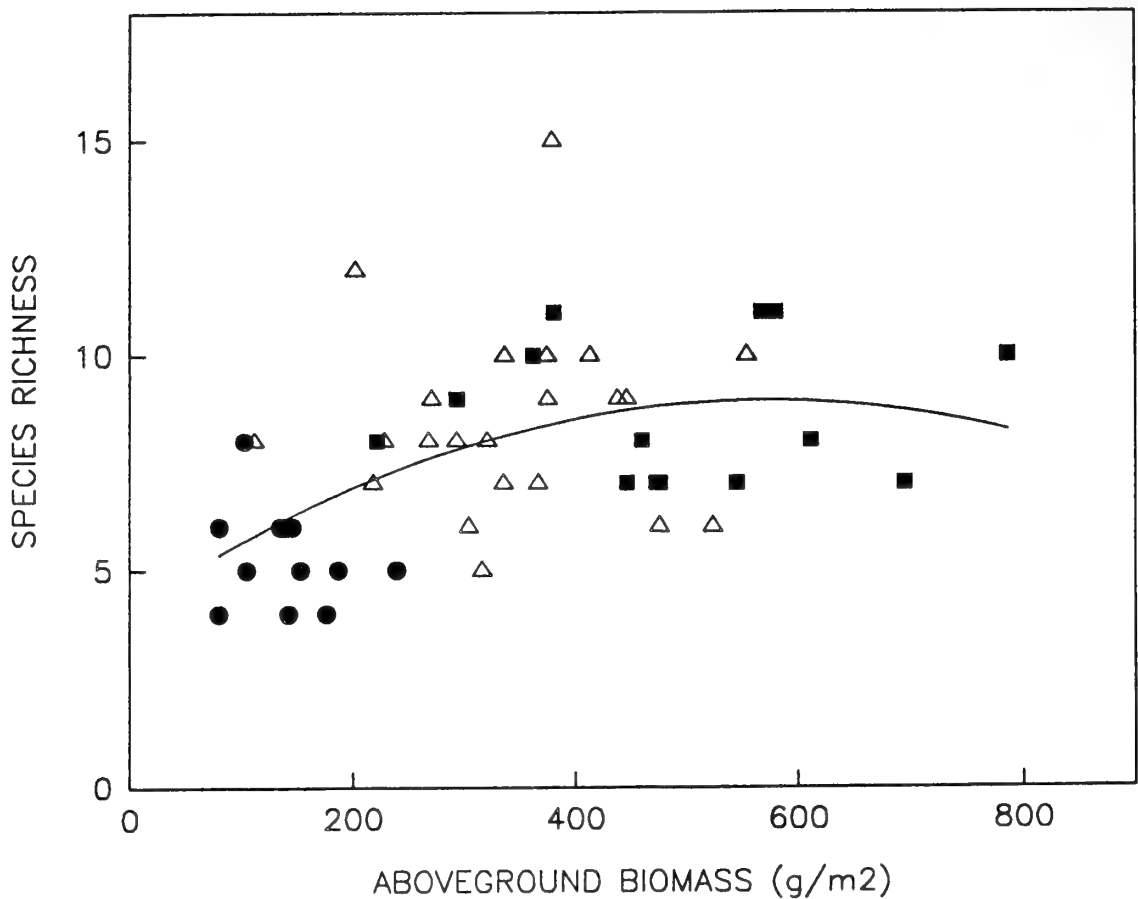
Fig. 6. Relationship between species richness (species number per 0.0625 m²) and aboveground peak biomass, and fitted second order polynomial regression. Symbols like in Figure 2.

(Marañón and Bartolome 1993) and reduces physiological performance (Parker and Muller 1982) of most grassland species.

Higher soil moisture in the understory during late spring may allow a longer growth persistence, and may favor some perennial herbs like *Elymus triticoides* and *Lathyrus vestitus*. In similar mediterranean-climate Southern Spain, perennial grasses *Dactylis glomerata, Lolium perenne* and *Festuca ampla* were found preferently under oak trees (Marañón 1986), favored by a reduction in the early summer drought stress (Joffre and Rambal 1988).

Higher inorganic nitrogen availability was also found in soils under deciduous *Quercus douglasii* (Jackson et al. 1990), although plant biomass was not affected. Soil ammonium and nitrate concentrations varied seasonally, and during the period of rapid growth (February–April) nitrate pools were almost depleted in the open grassland (Jackson et al. 1990).

Species composition under the oak canopy differs from the adjacent open grassland, as found by several authors in diverse conditions: isolated evergreen *Q. agrifolia* (Parker and Muller 1982), winter deciduous *Q. douglasii* (Holland 1980; McClaran and Bartolome 1989; Callaway et al. 1991; Bartolome and McClaran 1992)

and deciduous *Q. garryana* (Saenz and Sawyer 1986). Shade-tolerant species like *Montia perfoliata, Stellaria media* and *Galium aparine* seem to be excluded by competition from the dense open grassland, whereas light-demanding species like *Bromus mollis* and *Hypochoeris glabra* would not survive under closed evergreen oak canopy shade (Marañón and Bartolome 1993). A few species like *Bromus diandrus* and *Carduus pycnocephalus* have a wider ecological range and grow in both contrasted habitats.

Seasonal growth is slower in the understory reaching a lower peak standing crop than in the open grasslands, but the rapid decline in late spring is delayed under the oak canopy. A reduction in herbaceous biomass under evergreen oak was also found by Parker and Muller (1982). However, a variety of responses has been found under deciduous oaks: increasing biomass underneath (Holland 1980), decreasing (McClaran and Bartolome 1989; Bartolome and McClaran 1992) or no significant effect (McClaran and Bartolome 1989; Jackson et al. 1990). Global productivity of the system, oak trees plus herbaceous layer, should be considered for the management of this mosaic landscape (Jackson et al. 1990).

The edge of the oak canopy projection is the ecotone between two contrasted habitats: oak understory and open grassland. In this transition we would expect a higher species density (edge effect, Odum 1971), as found in other similar Mediterranean-climate systems (González-Bernáldez et al. 1969; Marañón 1986). Edge samples, in this study, had a combined species composition, and species density at the ecotone was higher than in the understory but similar to the open grassland. We suggest two reasons influencing the lack of a diversity peak at this ecotone: 1) The total pool of herbaceous species is lower than in the Mediterranean Basin precluding a fine-scale habitat separation. 2) Ungrazed local conditions, in the grassland studied, tend to favor dominant tall grasses and reduce alpha diversity (Heady et al. 1991).

Although the alpha diversity of the herbaceous understory was reduced by the oak canopy effect, the species composition varied compared to the open grassland (beta diversity) resulting in a greater species richness of herbaceous plants for the whole oak woodland-grassland landscape (gamma diversity). From a conservationist viewpoint, oak woodlands are refuges for low competitive, shade-tolerant, native species such as *Montia perfoliata,* in contrast with the open grasslands dominated by Euro-mediterranean colonizers.

At the oak canopy edge, herbaceous plants received a light incidence similar to the open grassland, and ameliorating oak canopy effects on soil moisture and nitrogen content. Peak standing crop is similar to the open grassland but the late spring decline is somewhat delayed. Biomass partitioning tends to be dominated by *Lolium multiflorum* probably benefiting from these peculiar environmental

TABLE 1. VALUES OF BIOMASS FOR MAXIMUM DIVERSITY (BMD) RECORDED BY DIFFERENT AUTHORS FOR HERBACEOUS COMMUNITIES.

Community-type (country)	Biomass for maximum diversity ($g\ m^{-2}$)	Reference
Fens (U.K.)	1500	Wheeler and Giller 1982
Annual grassland (Calif., USA)	570	This study
Herbaceous communities (U.K.)	510	Grime 1979
Wetlands (Netherlands)	400–500	Vermeer and Berendse 1983
Annual grassland (Calif., USA)	350	Bartolome et al. 1980, Heady et al. 1991
Chalk grasslands (Netherlands)	150–350	Willems 1980
Saltmarsh grassland (Spain)	302	García et al. 1993
Grasslands (Spain)	150–300	Puerto et al. 1990
Riverine wetlands (Canada)	300	Day et al. 1988
Lakeshore (Canada)	80–260	Wisheu and Keddy 1989

conditions. In growth experiments, *Lolium multiflorum* was a superior competitor than *Avena fatua* and *Bromus diandrus,* for high nutrient and high temperature treatments (Gulmon 1979).

The same four annual grasses (*Avena fatua, Bromus mollis, B. diandrus* and *Lolium multiflorum*) that dominated open grassland biomass samples, also dominated an ungrazed annual grassland studied in the Berkeley Hills (Ratliff and Heady 1962). Seasonal pattern and partitioning by species was also similar, although *Avena fatua* instead of *Bromus diandrus* was the dominant species. *Lolium multiflorum* had the longest weight persistence during early summer (Ratliff and Heady 1962).

Maximum species richness for an intermediate standing crop is a general trend found in many herbaceous vegetation types, although with different BMD values (Table 1). We found a unimodal relationship between biomass and species richness that supports the model of Grime (1979). The closed shaded habitat is a harsh (sensu Grubb 1987) light-limited environment for most herbaceous species; as a result a few shade-tolerant species form a grassland community of low species richness and low standing crop. In the open grassland, favorable amounts of water and nutrients may also reduce species richness by allowing dominance of tall grasses.

McNaughton (1968) found a negative correlation between species richness and productivity. His data set included highly-productive species-poor grassland on sandstone (similar to our open grassland community) that contrasted to low-productivity species-rich grassland on serpentine. Both light reduction and serpentine nutrient imbalance are harsh conditions reducing standing crop of the grassland community, but the ultimate effects on species diversity seem different. A high diversification of serpentine-tolerant plants is re-

flected in relatively species-rich communities (Kruckeberg 1984), but comparatively fewer shade-tolerant herbaceous species have evolved in Mediterranean climate, reflected in the species-poor understory communities.

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VEGETATION OF THE UPPER RAIDER AND HORNBACK CREEK BASINS, SOUTH WARNER MOUNTAINS: NORTHWESTERN LIMIT OF *ABIES CONCOLOR* VAR. *LOWIANA*

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Abstract

This study identifies the different plant communities and describes the forest stand structure in 2400 hectares of the upper Raider and Hornback Creek basins on the eastern slope of the South Warner Mountains in Modoc County, California. Major plant communites were estimated using aerial photography and ground reconnaissance. The predominant community in the study area was found to provide an example of a large contiguous stand (575 ha) of *Abies concolor* var. *lowiana* at the northeastern extreme of its distribution in California. Community structure was obtained from the point-centered quarter method and nested quadrats. Other plant communities identified were: Mountain Mahogany Scrub, Montane Meadows, Subalpine Sagebrush Scrub, Northern Juniper Woodland, Big Sagebrush Scrub, Whitebark Pine Forest, Washoe Pine-White Fir Forest, and Riparian Forest.

Few studies of the vegetation have been made within the Warner Mountains of northeastern California, and of those conducted, most have emphasized the vegetation of the western slopes or summarized habitat types (Pease 1965; Milligan 1969; Rundel et al. 1977; Vale 1977; Riegel 1982; Riegel et al. 1990). The vegetation of the eastern slopes of the Warner Mountains is less well-known. This study identifies the different plant communities present in a 2400 hectare area on the eastern exposure of the Warner Mountains. We also describe the structure of the dominant vegetation within this area, a large, relatively uncommon example of an undisturbed stand of mature *Abies concolor*. Here we hope to provide a framework for future ecological research regarding the regeneration and distribution of *A. concolor* as well as provide descriptive information about this understudied area.

Abies concolor is recognized as the dominant forest species in the Warner Mountains (Vale 1977; Riegel et al. 1990). However, much

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of the research conducted on white fir forests has been in the Sierra Nevada (Rundel et al. 1977; Conard and Radosevich 1982) with a few studies in the desert ranges of southern California (Vasek 1985). Based on existing research, *A. concolor* is found at mid-elevations both as a component of mixed conifer forests and in pure stands throughout its range. In northern California, white fir stands are frequently found at intermediate elevations between mixed conifer forests and red fir forests (Griffin 1967).

Abies concolor is shade-tolerant and, in the absence of fire, has become the climatic dominant over large acreages in Oregon and California. Mature stands of *A. concolor* have a closed canopy and very little understory vegetation. Stands are typically even-aged, with >80% of the overstory *Abies concolor* (Rundel et al. 1977; Shimamoto 1988). Understory associates are variable over the wide geographic range of the type.

Two varieties of *Abies concolor* have been recognized over the wide range of this species: *Abies concolor* var. *lowiana* in the Sierra Nevada and northeastern California, and *A. concolor* var. *concolor* in the Rocky Mountain region (Hamrick and Libby 1972). The Warner Mountain stands are among the largest, northeastern-most populations of *A. concolor* var. *lowiana* (Critchfield and Allenbaugh 1969).

Study Area

The Raider and Hornback Creek basins are located about 2.5 km northwest of Eagleville, California in the South Warner Wilderness Area within the Modoc National Forest (Fig. 1). The study area roughly delineated, comprises the upper watersheds of Raider and Hornback Creeks and occurs in Sections 3, 4, 8–10, and 15–22, Township 40 North, Range 16 East, Humboldt Base and Meridian, the Eagle Peak 7.5 minute quadrangle, Modoc County, California. The elevation of the study area ranges from 1480 m at the western edge of Surprise Valley to 2775 m at the top of Dusenbury Peak.

The Warner Mountains are a north–south block mountain range of the Modoc Plateau, formed as a result of dip-slip faulting (Oakeshott 1971). The Surprise Valley fault escarpment rises 1500 m above Surprise Valley and forms the eastern slope of the Warner Mountains. The eastern border of the South Warner Wilderness area generally follows the base of the escarpment.

Four major soil associations are present within the study area, with the Waca–Lyonman association supporting the majority of the vegetation. This deep and moderately deep well-drained soil in steep or strongly sloping areas supports *Abies concolor* and associated conifers (Camilleri 1979; Sheldon 1980). At lower elevations, the Homecamp–Newlands association is composed of stony and dark grayish brown loams and supports *Artemisia tridentata* and asso-
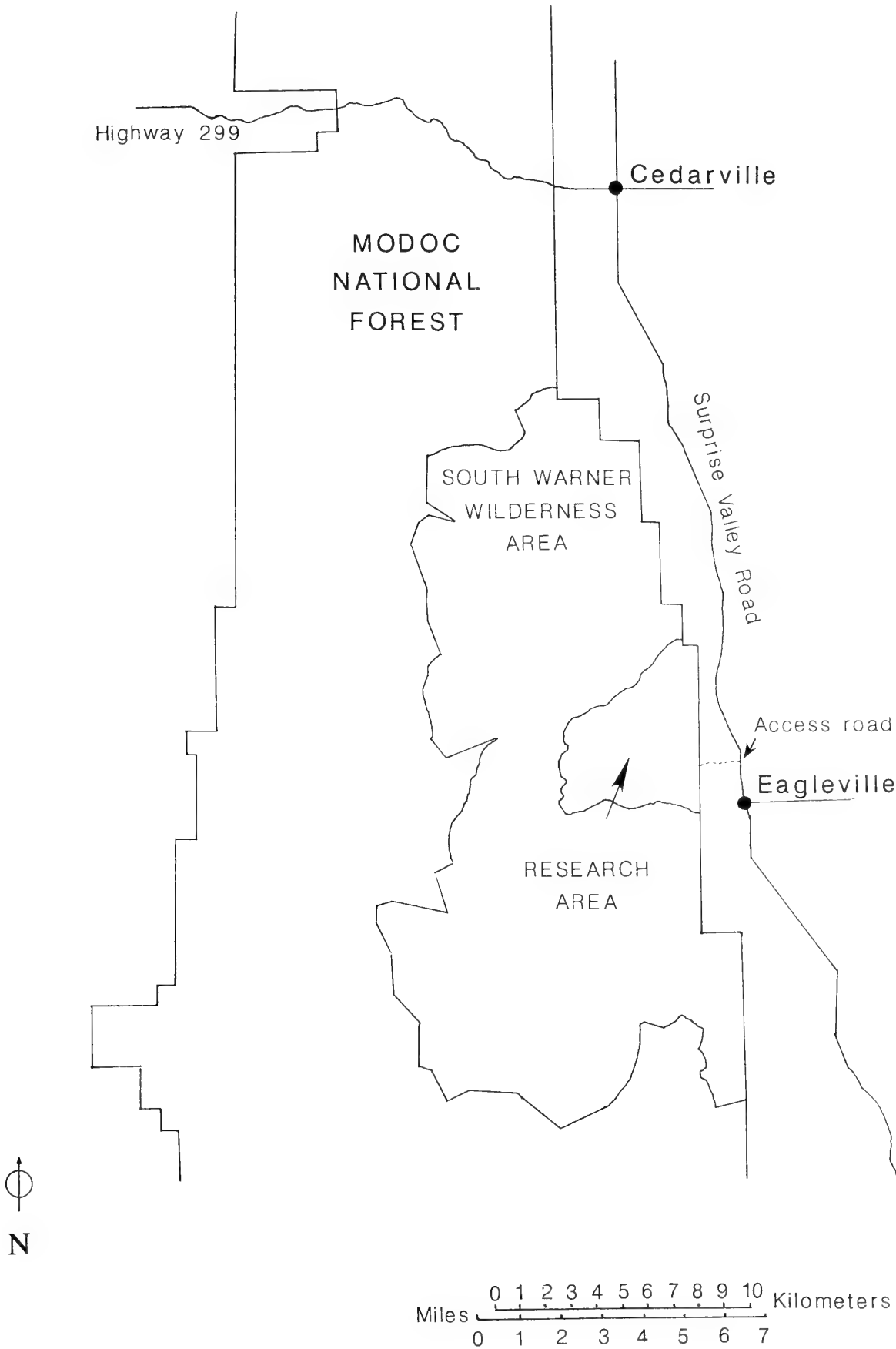
FIG. 1.   Map of study area in the upper Raider and Hornback Creek drainages, South Warner Mountains, Modoc National Forest, California.

ciated bunch grasses. The Hapgood–Snag association consists of deep, well-drained soils on mountain slopes and in small basins. It is comprised of dark grayish brown stony loam and gravely fine sandy loam over tuff and very stony fine sandy loam over slightly weathered basalt. The Hapgood–Snag association also supports *Artemisia tridentata* and various bunch grasses. The rocky outcrops and steepest portions of the study area are classified as the Rubble-land-Rock Outcrop association. Vegetation is sparse in these areas (Sheldon 1980).

The climate of the Warner Mountains is influenced both by precipitation patterns of coastal California and cold winter temperatures of the northern continental United States. These influences result in a climate of cold humid winters and virtually rainless, short, mild summers (Pease 1965). The annual precipitation in the study area is approximately 51 cm, the majority of it falling from September through mid-June in the form of snow. Winter days in which precipitation falls alternate with those that are extremely cold and dry. Dry thunderstorms are common during late May, June, and July, and occur on 20 percent of the days (Pease 1965). The mean January temperature of the eastern slope of the Warner Mountains is estimated to be −6.6°C, and the mean July temperature 15.5°C (Pease 1965).

Grazing and fire disturbances to the study area have been limited. Modoc National Forest personnel have no knowledge of any fire within the study area in the last 95 years (S. Smith personal communication). The Raider Creek basin was grazed by sheep until 1943 and by cattle from 1943 to 1971. The study area has had little use as a grazing allotment since 1971, although sheep allotments have been used in adjoining Owl and Mill Creek basins and some animals may have wandered into the Raider and Hornback Creek basins (Camilleri 1979). A lack of access to an adjoining cattle allotment due to storm damage required the movement of cattle through the study area in 1987. Cattle use of the Raider Creek trail in 1987 was authorized on a one-time basis (M. Yamagiwa personal communication). Although we found some evidence of erosion due to trampling at lower elevations outside of the study area, there was no apparent grazing related damage to vegetation within the study area.

Methods

The forest vegetation was sampled along four transects in the Raider Creek basin during August 8–14, 1988. Transect location was chosen following visual reconnaissance and aerial photograph examination to obtain the best representation of vegetation throughout the stand. Transects were evenly spaced approximately 1 km apart throughout the basin; precise locations can be found in Jensen and Schierenbeck (1989). Point-centered quarter method (Cottam

and Curtis 1956) was used to determine frequency, density, and basal area of the overstory trees. At 10 m intervals, distance and diameter at breast height (dbh) were measured for four trees at each of 21 points along three transects; a fourth transect had only 11 points. Running means were calculated along each transect to determine sampling adequacy (Mueller-Dombois and Ellenberg 1974). Only those trees >2 m in height were counted in the overstory. Percent cover and frequency were measured in nested plots. The shrub stratum was sampled at each point using a 4 m² grid, randomly assigned to the right or left of the transect line. Herbaceous vegetation was sampled at each point using a 1 m² grid.

The extent of each plant community was determined using stereo aerial color photography (1:25,000) in conjunction with the results of quantitative sampling and qualitative field observations. Acreage was estimated using a dot grid area scale.

One classification system does not currently exist for all communities we surveyed. Holland (1986) provided the most comprehensive alternative, except for those forest stands dominated by *Abies concolor*. Hence, we refer to stands dominated by *A. concolor* as White Fir Forest (Society of American Foresters 1954), while the remaining plant communities are classified according to Holland (1986).

Plant species were identified in the field when possible. Voucher specimens were collected of all species for which field identification was questionable. Nomenclature follows Munz and Keck (1968). Diploxylon pines (*Pinus jeffreyi* and *P. washoensis*) could not always be accurately separated, particularly when cones were not present. *Pinus jeffreyi* and *P. washoensis* are known to hybridize and there is some controversy over the distribution of these species in the Warner Mountains (Haller 1961; Riegel et al. 1990). When in doubt, we refer to all diploxylon pines as *Pinus jeffreyi/washoensis*.

RESULTS AND DISCUSSION

The results from qualitative observation and interpretation of the aerial photography indicate White Fir Forest is the most abundant vegetation type in the study area; over 575 hectares of the study area are dominated by *Abies concolor*. At the lower elevations, the *Abies concolor* dominated canopy intergrades with mature individuals of either *Pinus jeffreyi* or *P. washoensis*. At higher elevations, the canopy intergrades with *Pinus albicaulis* and *Pinus monticola*. Much of the study area below 1768 and above 2377 meters consists of rocky exposed volcanic tuff barren of vegetation. Plant communities present in addition to White Fir Forest are described in Table 1.

In the forest transects, *Abies concolor* far surpassed the other conifer species in frequency, density, and cover (Table 2). Of 293 trees measured, 266 were *Abies concolor*, 12 *Pinus albicaulis*, and 15 *Pinus*

TABLE 1. VEGETATION TYPES IN THE RAIDER AND HORNBACK CREEK BASINS, SOUTH WARNER MOUNTAINS, MODOC NATIONAL FOREST, MODOC COUNTY, CALIFORNIA.

Vegetation type	Topographic limits	Area (hectares)	Dominant species	Associated species
Big Sagebrush Scrub	1820–2120 m on exposed se facing slopes	73 ha	*Artemisia tridentata* *Purshia tridentata*	*Agropyron spicatum* *Bromus tectorum* *Festuca idahoensis* *Stipa occidentalis* *Oryzopsis* spp.
Northern Juniper Woodland	1646–2012 m on exposed slopes	145 ha	*Juniperus occidentalis* ssp. *occidentalis*	*Artemisia tridentata* *Purshia tridentata*
Washoe Pine–White Fir Forest	generally below 1981 m	16 ha	*Pinus jeffreyi/* *washoensis* *Abies concolor*	*Artemisia tridentata*
Montane Black Cottonwood Riparian Forest	along Raider and Hornback creeks above 1600 m	limited	*Populus trichocarpa*	*Pinus jeffreyi* *Prunus emarginata* *Rosa woodsii* *Salix scouleriana*
Montane Riparian Scrub	limited to high elev.	as stringers in rocky drainages	*Salix scouleriana*	*Veratrum californicum* *Carex microptera* aff.
Mountain Mahogany Scrub	dry south facing slopes, exposed ridges	94 ha	*Cercocarpus ledifolius*	*Juniperus occidentalis* *Artemisia tridentata* *Balsamorhiza sagittata* *Amelanchier pallida* *Artemisia arbuscula* *Chrysothamnus nauseous* *Ribes cereum*

TABLE 1. CONTINUED.

Vegetation type	Topographic limits	Area (hectares)	Dominant species	Associated species
Montane Meadows	along creek branches in level or gently sloping terrain	73 ha	*Veratrum californicum*	*Agrostis exarata* *Deschampsia caespitosa* *Carex microptera* aff. *Elymus glaucus* *Epilobium* sp. *Frasera speciosa* *Glyceria elata* *Hordeum brachyantherum* *Hypericum anagalloides* *Lupinus polyphyllus* ssp. *superbus* *Populus tremuloides* (above 2120 m) *Potentilla gracilis* *Trifolium cyanthiferum* *Veronica americana*
Subalpine Sage Scrub	intermittent at high elevation barren areas	sporadic on barren areas	*Artemisia arbuscula*	*Arenaria aculeata* *Sedum stenopetalum* *Eriogonum caespitosum*
Whitebark Pine Forest	above 2317 m	approx. 104 ha as pockets	*Pinus albicaulis*	

TABLE 2. FREQUENCY, DENSITY, AND DOMINANCE AND IMPORTANCE VALUES OF TREES IN THE UPPER RAIDER CREEK BASIN.

Species	Absolute frequency	Density (trees/100 m²)	Dominance (cm²/100 m²)	Relative density	Relative dominance	Relative frequency	Importance value
Abies concolor var. *lowiana*	100%	5.35	6918.84	91.6%	94%	74%	260.6
Pinus jeffreyi	19%	0.25	375.47	4.2%	5.1%	14%	23.3
Pinus albicaulis	15%	0.23	68.98	3.9%	0.9%	11%	15.8

TABLE 3. FREQUENCY AND COVER DATA FOR HERBACEOUS SPECIES FOUND IN 1 M^2 QUADRATS, IN WHITE FIR STANDS IN THE UPPER RAIDER CREEK BASIN.

	Transect 1	Transect 2	Transect 3	Transect 4
Percent of quadrats with herbaceous vegetation	57	19	67	60
Average percent cover	3.9	0.2	5.5	7.0

SPECIES PRESENT

	Frequency percentage	Relative frequency	Cover
ALL TRANSECTS			
Abies concolor (seedlings)	4.0%	3.0%	0.6%
Adenocaulon bicolor	1.0	1.0	0.3
Amelanchier pallida	1.0	1.0	3.3
Arnica cordifolia	20.0	16.0	14.6
Berberis repens	3.0	2.0	1.0
Collinsia parviflora	3.0	2.0	1.6
Geranium sp.	1.0	1.0	0.3
Grass-unknown	20.0	16.0	15.3
Hieracium albiflorum	15.0	12.0	15.6
Kelloggia galioides	4.0	3.0	2.7
Linanthus nuttallii	3.0	2.0	0.6
Lupinus caudatus	5.0	4.0	6.6
Onagraceae-unknown	1.0	1.0	0.3
Osmorhiza chilensis	4.0	3.0	3.3
Penstemon gracilentus	12.0	9.0	8.3
Poa pratensis	8.0	6.0	5.5
Polygonum sp.	3.0	2.0	0.7
Pyrola picta	8.0	6.0	1.7
Silene douglasii	1.0	1.0	0.3
Sitanion hystrix	5.0	4.0	2.3
Solidago canadensis	5.0	4.0	13.6
Trifolium wormskioldii	1.0	1.0	1.0
TOTAL	128	100	99.5

jeffreyi/washoensis. Basal area of *A. concolor* ranged from 30 m^2 per hectare to 106 m^2 per hectare. All but three of the saplings or seedlings sampled were *A. concolor*.

The stands we sampled could be assigned to the *Abies concolor/ Osmorhiza chilensis* habitat type described by Riegel et al. (1990). Canopy cover was nearly exclusively *A. concolor*. The herbaceous vegetation, characteristic of the habitat type, was very sparse. Rundel et al. (1977) reported understory cover in mature White Fir forests was seldom greater than 5 percent; measured herbaceous understory cover in Raider Creek basin ranged from 0.2 to 7 percent (Table 3). Species that occurred with high frequency in the herbaceous quadrat samples included *Arnica cordifolia, Hieracium albiflorum, Penstemon gracilentus, Osmorhiza chilensis,* and *Kelloggia galioides.*
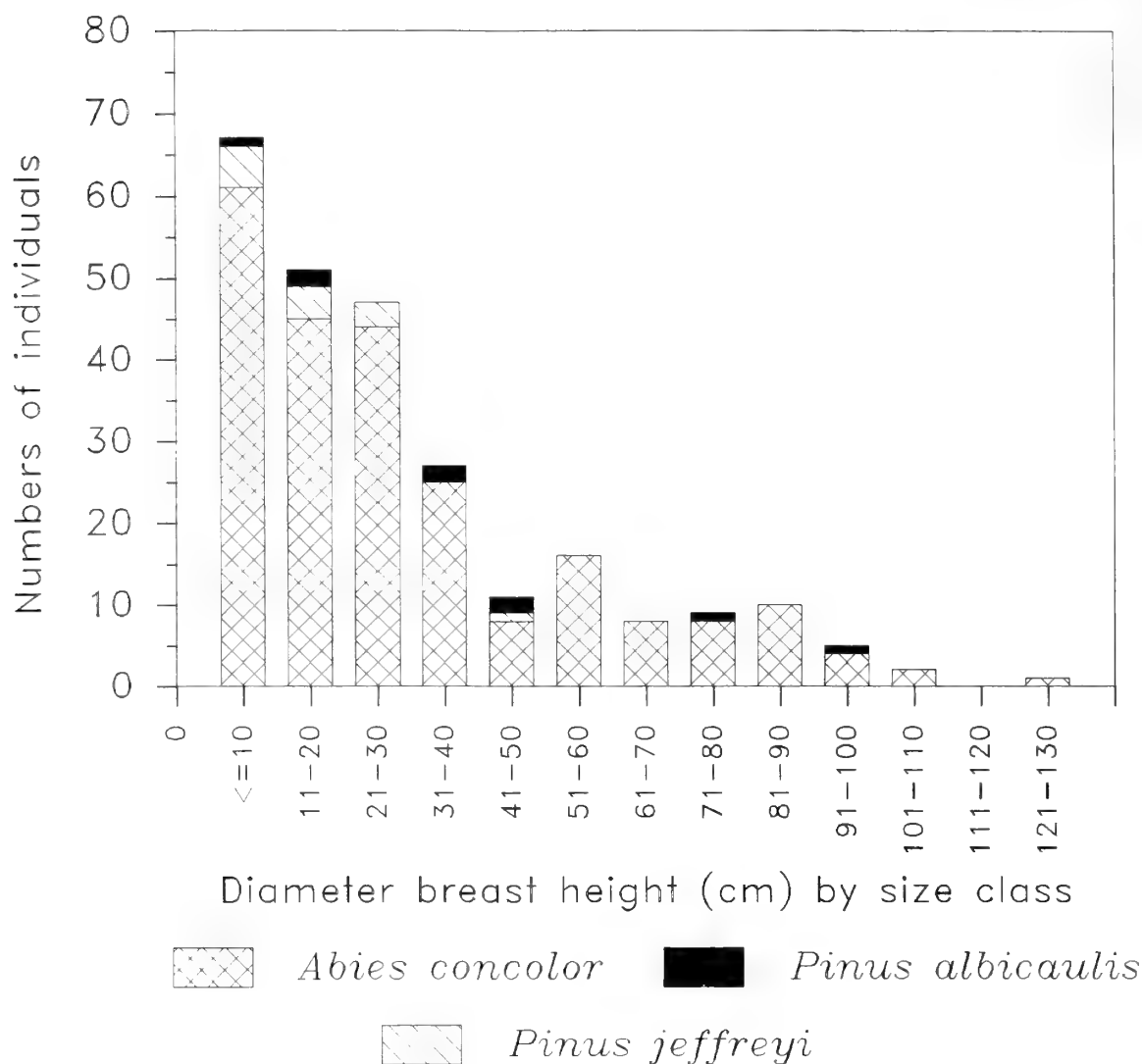
Fig. 2.   Size-frequency histograms of trees in the upper Raider Creek drainage.

Shrubby understory species were uncommon; 0.7, 0, 3.5 and 1.8 percent cover in the four transects, respectively (Table 3). The most common shrub species present was *Cercocarpus ledifolius.* Of the 177 plant species identified or likely to occur in the upper Raider and Hornback Creek basins (Jensen and Schierenbeck 1989), only 26 occurred in any of herb or shrub quadrats. Due to the elevational and topographic diversity and array of relatively undisturbed vegetation types within the study area, the flora of this often overlooked geographic region deserves more exploration.

Although the relationship between size and age in this study is unknown, size-frequency plots indicate that all of the stands show continuous regeneration and thus appear to be climax types (Fig. 2). The variation in size distributions may indicate that some portions of the basin contain older stands with less recruitment, while others have fewer large individuals and abundant recruitment. Although speculative, portions of the basin may have burned before the 1900's, while other stands were untouched. The size-frequency distribution

would be consistent with the scenario that the White Fir Forest of the Raider Creek basin is an aggregation of small stands that exist in a shifting mosaic of steady state reproduction (Pickett and White 1985). Alternatively, the reverse-J-shaped distribution by size classes may indicate a very old stand consisting of trees which die on a regular basis, release growing space and thus allow stems to invade at a uniform rate (Oliver and Larson 1990). Further research is necessary to determine the disturbance history and extrinsic factors which influence the dynamics of the basin vegetation.

Conard and Radosevich (1982) suggest that in the Sierra Nevada, mature stands of fire intolerant *A. concolor* are restricted to mesic sites with a low fire frequency. Despite the xeric nature of this site (Fowells 1965 reports 88.9–190.5 cm of annual water equivalent is typical for white fir stands), white fir is successfully reproducing. Lack of any recent large scale fire disturbance is supported by the low numbers of the more fire tolerant diploxylon pines. It is unclear whether the few diploxylon pines in the mid-elevation areas of the basin will remain in the continued absence of fire, with the possible exception of steep xeric slopes with low canopy cover of *Abies concolor*. The effects of the absence of fire and extensive grazing on the regeneration and structural composition of White Fir Forests await study in this area. Additional possibilities exist in the exploration of these individuals of *Abies concolor* var. *lowiana* as genetic resources for more xeric growing conditions.

The example of White Fir Forest in the upper Raider Creek basin is a mature, well-developed example of the type and offers a rare opportunity to study the ecological dynamics of *Abies concolor* without the influence of broadscale human or natural disturbance. Little quantitative data exist on White Fir Forests in California and it is our hope that the descriptive information provided here will serve as a backdrop for further research on their structure and reproduction.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

ARCTOSTAPHYLOS MANZANITA C. Parry (Ericaceae).—Tulare Co., open oak wood-land, Coffee Camp, Hwy 190, 8 km E of Springville, 600 m, 8 Oct 1993, *J. Keeley 251115–25121* (LOC).

Previous knowledge. Southern boundary of range recorded as central Sierra Nevada (P. V. Wells, *Arctostaphylos* in The Jepson Manual, University of California Press, Berkeley, 1993) or Mariposa Co. (P. A. Munz, A California Flora, University of California Press, Los Angeles, 1968).

Significance. Extends distribution over 150 km S to the southern Sierra Nevada. This southern-most population has several characteristics that are distinct from *A. manzanita* in Mariposa Co. and N. Branchlets and rachises are more densely to-mentose with slightly longer hairs and leaves are dull and sparsely tomentose. It is as distinct as other currently recognized subspecies although until further study it is best treated as the nominate subspecies.

—JON E. KEELEY, Department of Biology, Occidental College, Los Angeles, CA 90041.

NEVADA

JUNGERMANNIA CONFERTISSIMA Nees. (Hepaticopsida: Jungermanniaceae).—Wash-oe County, west flank of Mt. Rose, near junction of Mt. Rose trail and dirt road to microwave relay, cool shady north-facing streambank, base of slope at south end of large open meadow surrounded by open *Artemisia-Pinus contorta* woodland, 119°56′W, 39°19′N, elev. 2850 m, 19 Oct 1992. *A. T. Whittemore et al. 4171* (CAS, MO).

Previous knowledge. Circumboreal, at high latitudes and altitudes; in the western United States previously reported only from California.

Significance. New to Nevada.

SCAPANIA CURTA (Mart.) Dumort. (Hepaticopsida: Scapaniaceae).—Washoe Coun-ty, west flank of Mt. Rose, near junction of Mt. Rose trail and dirt road to microwave relay, shaded soil beneath grass, low bank above outlet of lake in large open meadow surrounded by open *Artemisia–Pinus contorta* woodland, 119°56′W, 39°19′N, elev. 2850 m, 19 Oct 1992. *A. T. Whittemore et al. 4165* (MO). Same locality, shaded north-facing streambank among *Pinus contorta, Whittemore et al. 4170* (CAS).

Previous knowledge. Circumboreal, south in western North America to California, Utah, and Colorado.

Significance. New to Nevada.

CHILOSCYPHUS POLYANTHOS (L.) Corda. (Hepaticopsida: Geocalycaceae).—Washoe County, west flank of Mt. Rose, near junction of Mt. Rose trail and dirt road to microwave relay, cool shady north-facing streambank, base of slope at south end of large open meadow surrounded by open *Artemisia-Pinus contorta* woodland, 119°56′W, 39°19′N, elev. 2850 m, 19 Oct 1992. *A. T. Whittemore et al. 4172* (CAS, MO).

Previous knowledge. Circumboreal, widespread in western North America, from the Arctic south to California, Utah, and Wyoming.

Significance. New to Nevada.

—ALAN T. WHITTEMORE, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299.

REVIEW

The Pines of Mexico and Central America. By JESSE P. PERRY, JR. 1991. Timber Press, Portland, Oregon. 231 pp. Hardcover, $35.95. ISBN 0-88192-174-2.

Within the borders of Mexico is the most diverse array of pines to be found anywhere in the world. Perry's book provides the first comprehensive coverage of these remarkable pines in almost thirty years and the first ever in english for a general readership. With the accumulation of much new information on Mexican pines in recent decades and the increasing threats to their existence, the arrival of this book is quite timely. The author provides a remarkable amount of field-oriented information and, especially because of this, the book makes a major contribution. However, it is flawed in both large and small ways that cannot be overlooked.

The book is divided into six chapters, following a format similar to that of *Los Pinos Mexicanos,* the pioneering work of Maximino Martinez published in 1948. The introductory chapter summarizes the chronology of the arrival and spread of pines in North America, and provides an overview of the topography and climate of Mexico and Central America. The second chapter focuses on classification, including a brief introduction to taxonomic rules, a description of characters useful for identifying pines, and the presentation of the author's taxonomic treatment of the Mexican and Central American pines. Beginning with a key to the subsections, the third chapter comprises the largest portion of the book, and includes a detailed, illustrated description of the taxa down to the level of forma. The fourth through sixth chapters include a summary of the current precarious status of Mexican and Central American pine forests, a brief highlighting of rare and endangered taxa, and the author's concluding remarks.

Forty years of observation and study have enabled Perry to produce an impressive volume. In addition to his own extensive work, he does a good job of including and discussing (but not always following) the results of numerous other recent analytical and taxonomic studies. The first-hand accounts of the morphology and natural history of all of the taxa over most of their geographic ranges in Mexico and Central America are the strongest part of this book. For example, I didn't realize that *Pinus leiophylla* and *P. occarpa* are "sprouters" following fires (unusual for pines), and that *P. michoacana* and *P. montezumae* have a juvenile "grass stage," similar to that of some of the pines in the southeastern U.S. The author frequently emphasizes the great variability of mexican pine taxa and the likely role of hybridization in adding to it. In his concluding remarks he shows his appreciation and concern for the future of this storehouse of variability, describing it as a "quite remarkable and infinitely precious natural experiment."

The introductory chapter provides some useful background, but has too many small errors and inconsistencies. The section on the origin of pines in North America is oversimplified to the point of being almost misleading; several problematical events are stated as fact. The section on the mountain ranges needs its own map. The rather detailed descriptions are hard to follow without one. In the section on climate the high peaks are called boreal instead of alpine, the annual precipitation in the Sierra Madre Occidental is given as 500–1000 mm in the text and as 1000–1500 mm on the accompanying map, and it is not made clear that the mountains of northern Baja California receive precipitation primarily in winter, not in summer like the rest of Mexico. Later in the book, the winter precipitation in these mountains is estimated as 15–30% of the annual total, but the actual percentage must be 70–90%.

The chapter on classification includes descriptions of characters, along with very helpful drawings that illustrate and compare the special morphological features of pines. However, following the practice of a long line of foresters, Perry refers to the immature cones as staminate and pistillate flowers. They are not flowers, and I object! Probably of less importance, Perry cites the Linnaean system as an example of a

natural system of classification, which it isn't. The example given for categories of classification uses the obsolescent Division Spermatophyta and Subdivision Gymnospermae, then skips the rank of class, formerly the practice with gymnosperm categories. The author's concept of the infraspecific variety is also dated, treated as an appendage to the "main" species, rather than one of two or more equivalent entities. A table summarizing Perry's classification of Mexican and Central American pines ends the chapter. In this table *Pinus pseudostrobus* is divided into five varieties and forms, three of which are placed in Subsection *Pseudostrobus,* while two are placed in Subsection *Oaxacana.* Because subsections outrank species, the Rules of Nomenclature don't allow such a disposition, which violates the hierarchical structure of formal classification. This same misclassification is carried over into the next chapter, where the varietal descriptions of *P. pseudostrobus* are again divided between two subsections.

Each taxon is described at length in the third chapter, including photographs of its habit, bark, foliage, and cones, as well as a range map. Numerous tables compare the morphological and occasionally the chemical characters of related taxa. These tables can be both helpful in making some difficult distinctions and frustrating in the amount of overlap and lack of resolution that they occasionally reveal. Following the description of each taxon are explicit directions to localities where good examples of native stands may be found. These should be valuable in the field, but I found the description of many of the poorer roads as "trails" to be a bit confusing. This chapter gets off to a shaky start with a key to the subgenera, sections, and subsections that is unworkable in spots. Couplets seem to be missing in at least three places, producing "blind alleys" in the key. In one place a couplet gives the choice of cones 8–15 cm long vs. cones 2–8 cm long. If the latter choice is taken, the next couplet offers cones 5–12 cm long vs. cones 20–35 cm long! Perhaps these particular problems are the result of a series of misprints, which should have been caught in any case. There is no key to the species or the infraspecific taxa. This lack is only partially compensated by the comparison tables that accompany the descriptive material.

I had many other problems with Chapter three. Some result mainly from differences of opinion with the author, but numerous questions remain. I will summarize my main concerns and offer a few specific examples. While a number of obviously distinct new species of Mexican pines have been recognized by various authors over the last few decades, and I appreciate Perry's work in bringing them together in this volume, he has probably recognized too many taxa at levels that are too high. If the criteria used here were applied to *Pinus ponderosa* and *P. contorta* in the U.S., each could be subdivided into a half-dozen full species and who knows how many infraspecific entities. In several cases Perry is simply accepting, relatively uncriticially, the work of others (Martinez, Loock, Mirov, Passini) but he also has authored a couple of questionable taxa. His descriptions of "different" taxa often overlap very broadly, leaving little, if anything, that is distinct. Aside from linear measurements, there are no quantitative or statistical data presented. While such data may not be appropriate for this book they often don't exist elsewhere. However, J. W. Stead and B. T. Styles, among others, have studied the relationships of some of the Mexican pines using principal components analysis and canonical distribution analysis. As a result, they have reduced several species to infraspecific taxa or to synonomy. Perry disagrees. He relies heavily on turpentine chemistry for distinguishing some of the taxa. While such chemical characters can be quite useful, the differences cited are based on very limited studies and cannot be considered definitive. In other situations where taxa that are treated as distinct have sympatric ranges and are difficult to distinguish, Perry assumes that extensive hybridization is occurring. I'm certain that this does occur, but Perry doesn't consider the alternative interpretation: a single taxonomic entity showing high variability at the population and regional levels. Several of his descriptions strongly suggest this to me.

Continuing with Chapter three, I'll note just a few apparent misinterpretations and inconsistencies. *Pinus contorta* is placed in the author's Section *Serotinae* ("closed

cone" pines) even though his key states that the cones are "not serotinous". They are not even persistent in subsp. *murrayana,* the only subspecies that extends into Mexico. *Pinus murrayana* has obvious close affinities with *P. banksiana* of boreal North America, but there is no evidence to support the close linkage of *P. contorta* to any of the other Mexican pines. *Pinus flexilis* may or may not occur in Nuevo Leon, but Perry's evidence is unconvincing and his description is inconsistent: height 20–40 m, leaves flexible (p. 43); height 7–15 m, leaves stiff (p. 45). The photograph of the cone resembles *P. strobiformis,* which the author cites from the same area, more than *P. flexilis.* Perry recognizes 12 Mexican species in his Subsection *Cembroides* (piñon pines). Several of these seem to be based on slender evidence. For example, *P. quadrifolia* and *P. juarezensis,* apparently sympatric in the mountains of northern Baja California, are supposed to be distinguished by their needle number: often 4 per fascicle, but commonly 3 or 5 in *P. quadrifolia,* and usually 5, but occasionally 4 in *P. juarezensis.* However, Perry's photographs show more 5-needle fascicles than 4-needle fascicles in both species. Needle number per fascicle is variable within many pine species. My own work with *P. ponderosa* indicates that needle number is often affected by environmental factors and can change from one year's growth to the next on the same branch. Other questionably distinct species, not convincingly supported by Perry's description, include *P. strobiformis-P. ayacahuite* var. *brachyptera, P. remota-P. catarinae, P. johannis-P. discolor, P. cembroides-P. lagunae, P. leiophylla-P. chihuahuana, P. arizonica-P. durangensis, P. hartwigii-P. rudis-P. donnell-smithii, P. pseudostrobus-P. estevezii-P. oaxacana,* and *P. oocarpa* var. *ochoterenai-P. patula* var. *longipedunculata-P. tecunumanii.*

Chapters four and five relate the generally sorry condition of pine forests in Mexico and each of the Central American countries with native pines. Here and in most other parts of the book, fire is regarded primarily as a destroyer of pine forests, which it often is, but the role of fire in maintaining pine-dominated ecosystems is not stressed sufficiently. Perry emphasizes that the primary destructive factor in the pine forests is over-exploitation by humans, driven by population pressure. This important point is underscored by colorful, even apocalyptic rhetoric. It is noted that "we" could help the people of Mexico and Central America to save their pines, but nothing specific is suggested. I would have hoped that, with 40 years of experience in the region, Perry might have more to offer. There is also no mention of current conservation efforts within Mexico and Central America. While still far short of sufficient, they should be highlighted and specifically encouraged in a book such as this.

The bibliography that concludes the book includes a good combination of old and recent references, including many from relatively obscure sources. In spite of its shortcomings, I would buy this book and use it with caution. It's full of information and should be a valuable companion in the field.

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Ecosystems of the World 8A. Natural Grasslands. Introduction and Western Hemisphere. Edited by ROBERT T. COUPLAND. Elsevier, New York, NY. xiii + 469 p. Hardcover, $217. ISBN 0444-88264-2.

This is the first of a two-volume series dealing with grasslands of the world; Volume 8B covers grasslands of Europe, Africa, Asia and Oceania. While Volume 8A concentrates on North America and South America there is much information on climate, soils and general ecological processes.

One chapter relevant to Madrono readers is the "California Prairie" contributed by H. F. Heady et al. This chapter includes some new material not covered in Heady's

contribution to the *Terrestrial Vegetation of California* book (edited by Barbour and Major). The present contribution, however, is an outdated coverage of the subject, finished years before the 1992 publication date. While it represents a useful summary of many important studies performed by UC Davis and UC Berkeley scientists, it includes few other studies. It is noted that, while the authors included more than 20 of their own papers, none of the work performed on Jasper Ridge grasslands in the past two decades is cited; the omission of names such as Gulmon, Mooney, Turitzin, Chiariello, and Hobbs, when discussing California grasslands, is inexcusable. Not only were most all papers dealing with southern California grasslands omitted, but southern California grasslands were omitted from the distribution map. This chapter falls short of being an adequate review of the California Prairie. Not being familiar with literature on other western North American grasslands I can not say whether this problem is true of other chapters in the book. In light of my disappointment with the California grassland chapter, I cannot suggest this volume as an addition to our reader's library.

—Jon E. Keeley, Department of Biology, Occidental College, Los Angeles, CA 90041.

ANNOUNCEMENT

Beginning 1 January 1994, all new manuscripts and correspondence concerning previously submitted manuscripts should be addressed to the new editor:

Dr. Robert Patterson
Department of Biology
San Francisco State University
San Francisco, California 94132

ANNOUNCEMENT

New Publications

A Flora of the Vascular Plants of Mendocino County, California. By Gladys L. Smith and Clare R. Wheeler. 1992. Wasmann Journal of Biology (Vols 48/49, nos. 1 and 2), University of San Francisco, San Francisco, CA. 387 p. Softcover, $22.95. Covers 2746 taxa and identifies floristic habitats, parks, preserves and special ecological areas. Includes early history, botanical explorations and geological background.

Paramo. An Andean Ecosystem under Human Influence. Edited by H. Balslev and J. L. Luteyn. 1992. Academic Press, San Diego, CA. xiv + 282 p. Hardcover, $59. ISBN 0-12-460442-0. Twenty-one chapters contributed by northern European botanists and ecologists on various plant groups and fire ecology of the northern Andes alpine environment.

Ecosystem Experiments. Edited by Harold A. Mooney, Ernesto Medina, David W. Schindler, Eernst-Detlef Schulze, and Brian H. Walker. 1991. John Wiley & Sons, New York, NY. xxvi + 268 p. Hardcover, $148.50. ISBN 0-471-92926-3. Fifteen different ecosystem experiments, both natural and planned experiments.

The Dictionary of Ecology and Environmental Science. Edited by Henry W. Art. 1993. Henry Hold and Company, New York, NY. viii + 632 p. Hardcover, $48. ISBN 0-8050-2079-9. Extensive enough to be of use to most scientists as well as lay persons.

Advances in Computer Methods for Systematic Biology. Artificial Intelligence, Databases, Computer Vision. Edited by Renaud Fortuner. 1993. Johns Hopkins University Press, Baltimore, MD. xiv + 560 p. Hardcover, $65. ISBN 0-8018-4492-4. Thirty chapters contributed by a diverse collection of scientists in areas of "Systematic Biology and Phylogenetic Inference", "Expert Systems, Expert Workstations, and Other Identification Tools", "Database Systems", and "Computer Vision and Feature Extraction".

Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. By Edward A. Johnson. 1992. Cambridge University Press, New York, NY. xiii + 129 p. Hardcover, $49.95. ISBN 0-521-34151-5. Although a thin book, this is a surprisingly complete coverage of all aspects of fire in the boreal forest in North America.

ANNOUNCEMENT

Botany on the Smithsonian Institution's
Natural History Gopher Server

The Smithsonian Institution's *Gopher Server* has recently added two important offerings of interests to botanists. The **Type Specimen Register of the U.S. National Herbarium**, which with over 88,000 records, is the world's largest electronic database of plant type specimens. The **Index to Historical Collections** is the most comprehensive account of collectors represented in the U.S. National Herbarium. At present the same Gopher Server provides electronic access with key word search capability to several additional documents, including the **Biological Conservation Newsletter** (1981–present), and the **American Society of Plant Taxonomists Newsletter** (1987–present). Resources are also available in vertebrate zoology and molecular systematics. All of these services are accessible on the Internet.

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Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or "erasable" paper. Avoid footnotes except to indicate address changes. Abbreviations should be used sparingly and only standard abbreviations will be accepted. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

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All members of the California Botanical Society are allotted five free pages per volume in Madroño. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing Madroño on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

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Contents

NATURAL CONDITIONS FOR SEEDLING EMERGENCE OF THREE WOODY SPECIES IN THE NORTHERN SONORAN DESERT

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Abstract

Seedling emergence of *Cercidium microphyllum, Fouquieria splendens* and *Encelia farinosa* was monitored on Tumamoc Hill, Tucson, Arizona, during eight years. *Cercidium* and *Fouquieria* emerged in response to warm-season rains. *Encelia* emerged in the cool season. Minimum rainfall triggers for emergence were: *Cercidium,* 17 mm; *Encelia,* 19 mm; *Fouquieria,* 25 mm. Given a large enough rain trigger during the correct season, emergence of *Encelia* and *Cercidium* depends further upon appropriate *minimum* temperatures. *Encelia* failed to emerge in winters when the absolute minimum temperature during the 9 days after the trigger fell below freezing. On all but one occasion, *Cercidium* emergence failed when average minimum temperatures within 3 days of the trigger fell below 20°C. Multiple emergence events (more than one emergence in a single season) were observed in *Cercidium* and *Encelia.* After three emergence pulses, 43 percent of the initial *Encelia* seed bank remained in the soil. After two emergence pulses, 28 percent of the *Cercidium* seed bank was left. Both species evidently have persistent seed banks. *Fouquieria* seeds do not persist in the soil.

Information on natural germination conditions is basic to a full knowledge of the ecology of a plant species or population (Grime 1979). Studies of natural conditions for germination and emergence may lead to a better understanding of community composition and plant demography, especially in deserts, where emergence may be episodic (Shreve 1917; Barbour 1968; Sheps 1973; Ackerman 1979; Sherbrooke 1989). Knowledge of natural germination requirements is essential for modeling seed banks (Simpson et al. 1989), but while interactions among germination requirements, emergence events and seed dormancy have been extensively investigated for desert annuals (e.g., Went 1948, 1949; Went and Westergaard 1949; Wilcott 1974; Venable and Lawlor 1980; Venable 1989), comparable information is not available for woody desert species.

Laboratory studies of seed germination, which typically manipulate temperature but not moisture, can readily demonstrate the optimum temperature for germination but rarely elicit moisture requirements. In deserts, where rainfall is highly variable, such knowledge is crucial to predicting how often germination and emergence are likely to occur in nature. This study reports on natural germination conditions for three common and characteristic woody spe-

cies of the northern Sonoran Desert: *Cercidium microphyllum* (Torr.) Rose & Johnston (Fabaceae: Caesalpinioideae), *Fouquieria splendens* Engelm. (Fouquieriaceae), and *Encelia farinosa* A. Gray (Asteraceae). Given favorable climatic conditions, seedlings of these three species can emerge in large numbers: several hundred seedlings/m^2 for *Fouquieria* (Shreve 1917), 5 seedlings/m^2 for *Encelia* (Goldberg and Turner 1986), and about 1 seedling/m^2 for *Cercidium* (Shreve 1917).

Germination can be considered as a phenological event, that is, a temporal phenomenon stimulated by certain climatic or environmental triggers. Among the many factors known to trigger germination are temperature, moisture, light intensity, light quality, photoperiod, carbon dioxide and minerals (Rathcke and Lacey 1985). Laboratory studies suggest that, for the 3 species considered here, moisture and temperature are the paramount triggers. *Fouquieria splendens* germinates equally well in light and darkness, and achieves nearly 90 percent germination at 20–25°C. At these temperatures, germination takes 5–8 days. The seeds can germinate within a much wider range of temperatures (10–40°C) (Freeman 1973; Freeman et al. 1977). *Encelia farinosa* germination occurs at temperatures as low as 15.6°C (Shreve et al. 1937) and as high as 30°C (James Ehleringer, personal communication). Best results are obtained when the seeds are kept at or near the soil surface and sprayed frequently with water; germination takes 7–10 days in the laboratory (James Ehleringer, personal communication). Poole (1958) obtained 88 percent germination of *Cercidium microphyllum* at 15–18°C; highest germination of the sympatric *Cercidium floridum* occurred at 21–30°C. Laboratory germination of *Cercidium microphyllum* required 2 days (Poole 1958).

The goals of this study were, first, to assess the relative importance of various temperature and moisture levels in stimulating natural germination and emergence of *Encelia, Cercidium* and *Fouquieria* on Tumamoc Hill, Tucson Mountains, Arizona, and second, to determine whether multiple emergence events deplete the seed banks of these three species. Specific questions addressed were: 1) what is the smallest amount of rain that can trigger germination and emergence; 2) do moisture conditions in the days before and after the trigger affect germination and emergence; 3) do temperature conditions in the days before and after the trigger affect germination and emergence; and 4) what proportion of seeds, if any, remains in the seed bank after multiple emergence events?

Study Area

The Tumamoc Hill study site (32°13′N, 111°05′W) is at 814 m on a gently sloping bench with a northeast aspect. Tumamoc Hill,

an outlier of the Tucson Mountains, lies from 703 to 948 m in elevation. Its rocky, basaltic-andesitic slopes are dominated by the 3 study species as well as by *Larrea tridentata, Carnegiea gigantea, Ambrosia deltoidea, Opuntia engelmannii* and other woody perennials characteristic of the Arizona Upland division of the Sonoran Desert. Daily maximum and minimum temperatures have been recorded on Tumamoc Hill from 1907 to 1939, 1943 to 1956, and 1976 to the present. The precipitation record extends from 1907 to the present. Annual rainfall averages 25.0 cm. Almost half of it falls during July, August and September; most of the remainder arrives between October and April (Goldberg and Turner 1986).

METHODS

Field observation. Dates of emergence for *Cercidium, Encelia* and *Fouquieria* came from two sources. From 1985 to 1989, I observed mass emergence of *Cercidium* and *Encelia* several times while making twice-monthly observations for a phenology study on Tumamoc Hill (Bowers and Dimmitt, in prep.). Additional data for these two species and for *Fouquieria* came from a 557 m² plot on the north slope of Tumamoc Hill where, starting in September 1987, Raymond M. Turner, Tony L. Burgess and I tagged and numbered all seedlings of all woody perennials for a plant demography study. This study is still underway and will be analyzed and presented separately. Because the phenological observations were made at 2-week intervals, and the demography plot was examined only 2 or 3 times a year, the observed dates of emergence occasionally lagged behind the actual dates by several weeks.

Climatic variables. The object of this study was to identify the climatic conditions under which germination and emergence had occurred, then compare them with conditions under which germination and emergence had not occurred.

The weather record was examined to identify the likeliest trigger (defined as the smallest single rain capable of stimulating emergence) for each event. Isolated rains not followed by emergence were useful in identifying the minimum trigger. In most cases, it was quite clear that some rains were too small to have triggered germination and that others, while large, were too close to or too far from the emergence date to have done so. When there was some doubt, such as two large rains close to the time of emergence, I chose the first of the two. For *Encelia,* I then tabulated the following climatic factors for the 9 days before and after each potential trigger: total rain, average maximum temperature, average minimum temperature, absolute minimum temperature and absolute maximum temperature. (Nine days was the shortest time required for emergence on Tu-

mamoc Hill.) The same calculations were repeated for 24 days before and after each potential trigger. (Twenty-four days was the longest time required for emergence on Tumamoc Hill.) I treated *Cercidium* the same way, selecting first the most probable trigger for each emergence event from May 1985 to October 1991, generally the first heavy rain (≥ 17 mm) of the summer, then tabulating the same climatic factors for the three days before and after each potential trigger. (Two to three days are required for germination in the wild and in the laboratory.)

Next, I assembled comparable climatic data sets in which no emergence had occurred. For *Encelia,* all potential triggers from October 1985 to April 1992, except for those that had triggered emergence, were selected. For *Cercidium,* all potential triggers from May 1985 to October 1991 were selected, again omitting those that had triggered emergence. For each rain event, I compiled the same climatic factors as for the emergence data sets.

Finally, using the 10 climatic variables as independent variables and the presence or absence of emergence as the dependent variable, I employed a discriminant analysis procedure to examine the relative contribution of rain and temperature to the emergence of *Encelia* and *Cercidium.*

For *Fouquieria splendens,* the heaviest single rain in the 2 weeks before emergence was selected as the probable trigger. There were too few emergence events for a meaningful discriminant analysis.

Encelia seed bank. On April 8–10, 1992, 30 microsites were sampled to determine the viable *Encelia* seed bank for winter–spring 1991–1992. The microsites were situated as follows: 10 on open, bare ground; 10 under canopies of *Encelia* where no *Encelia* seedlings had emerged; and 10 under *Encelia* canopies where *Encelia* seedlings had emerged. Each microsite was a circle with an area of 227 cm². To sample the microsites, I placed a circular wooden frame on the ground, then counted the number of recently germinated *Encelia* seedlings in each. Next, I removed the top 2–3 cm of soil inside the frame, putting the sample into a plastic bag. Each sample was sifted through a coarse sieve (3.35 mm mesh) to winnow out rocks and debris, then through a fine sieve (0.833 mm mesh) to retrieve all *Encelia* seeds (mean seed length = 4.5 mm, n = 50). Finally, the seeds were examined to determine viability. Those that had not filled or were broken, cracked or infected were clearly not viable. The seeds that were plump and firm proved, upon opening, to contain fully developed embryos; I considered all such seeds to be viable. The viable seed bank for winter–spring 1991–1992 was determined by adding the number of recently emerged seedlings to the number of viable seed left in the soil.

Cercidium seed bank. On August 13, 1993, similar methods were used to determine the viable *Cercidium* seed bank for summer 1993. Fifteen 227 cm² microsites were located where *Cercidium* seedlings had emerged in response to rains totaling 1.11 cm on August 8–9; 15 adjacent microsites were placed where no seedlings had emerged. Seedling clusters showing signs of predation (gnawing and excavation of seedlings) were avoided. I removed the top 4–5 cm of soil from each site, then, using 8.00 mm and 0.833 mm screens, sieved the samples to retrieve all *Cercidium* seeds (mean seed length = 9.0 mm, n = 50). All the retrieved seeds were plump, firm, and apparently viable. On August 17, 1993, 4 days after a 17-mm rain triggered another pulse of emergence, I repeated the entire sampling process. The viable seed bank for summer 1993 was considered to be the number of seeds in the soil plus the number of recently emerged seedlings at the time of the first sampling.

For both *Encelia* and *Cercidium,* the sampling method was intended to determine what proportion of seed remained in the soil after multiple emergence events, not to characterize the temporal or spatial variability of the soil seed bank.

Fouquieria seed bank. Because recently emerged *Fouquieria* seedlings were observed only on the seedling demography plot, where they could not be disturbed, I could not determine the viable seed bank in the same manner as for *Encelia* and *Cercidium.* Instead, I inspected the soil surface for recently dispersed *Fouquieria* seeds on June 7, 1993, at the peak of seed dispersal, and again a week later, when most of the capsules were empty. I also noted presence or absence of *Fouquieria* seed in the *Encelia* and *Cercidium* seed-bank samples.

Results

Field observations. From 1985 to 1992, recently emerged seedlings of *Cercidium* were observed on July 18, 1985; September 2, 1986; August 14, 1987; September 15, 1987; August 3, 1988; September 2, 1988; August 4, 1989; October 24, 1989; August 8, 1990; and August 27, 1991. Seedling size and presence or absence of cotyledons suggested that these 10 dates represented 13 different emergence events. During the same period, new *Encelia* seedlings were recorded on December 17, 1985; April 4, 1987; November 8, 1988; October 24, 1989; February 7, 1992, March 5, 1992, April 5, 1992; and December 27, 1992. *Fouquieria splendens* emergence was recorded on September 11, 1987; October 19, 1989; and August 8, 1990.

Substantial numbers of *Encelia* and *Cercidium* emerged at every event. On February 25, 1992, for example, there were 439 *Encelia*

seedlings on our 557 m² demography plot. On August 27, 1991, we found 327 *Cercidium* seedlings. In contrast, emergence of *Fouquieria* was sparse; fewer than 5 seedlings were seen on any one date.

Climatic variables. Examination of the Tumamoc Hill weather record suggested that minimum rainfall triggers for the 3 species are: *Cercidium,* 17 mm; *Encelia,* 19 mm; *Fouquieria,* 25 mm. Both *Encelia* and *Cercidium* are capable of germinating in response to the first heavy rain that ends a virtually rainless period of 8 weeks or longer. Germination and emergence may be slower in the wild than in the laboratory, especially under cool winter temperatures. *Encelia* seedlings at the cotyledon stage were observed on Tumamoc Hill as early as 9 and as late as 24 days after the apparent trigger. *Cercidium* seedlings were observed as early as 3 days after a triggering rain. Shreve (1917) also reported *Cercidium* emergence within 3 days.

For *Encelia,* there were 8 triggering rains. Nine other rains of equal or greater magnitude did not trigger emergence. Of the 21 rains large enough to trigger *Cercidium* germination, 13 did so. In spring 1992, *Encelia* had 3 pulses of germination. *Cercidium microphyllum* had 2 emergence pulses in each of 5 different summers. *Fouquieria* emergence was observed only 3 times, although rains large enough to trigger emergence occurred 13 times in 7 different summers.

Discriminant analyses. Precipitation and temperature within 24 days of the trigger had no effect on *Encelia* emergence (Table 1). Most of the climatic variables within 9 days of the trigger also had no effect. The notable exception was absolute minimum temperature after the trigger, which was significantly related to emergence. For *Cercidium,* there were significant relations between emergence and each of the following variables: average minimum temperature before the trigger, average minimum after the trigger, absolute minimum before the trigger and absolute minimum after the trigger (Table 1).

Encelia seed bank. The 30 microsites had 122 *Encelia* seedlings and 91 viable seeds, an initial viable seed bank of 213 in 6810 cm², or 313 seeds/m². Most of the seedlings and seeds were concentrated under the canopies of *Encelia* plants. At the time of sampling, about 1 month before fresh seed was dispersed, 43 percent of the initial viable seed bank remained in the soil. The large fraction of seed remaining in the soil so long after dispersal indicates that *Encelia* has a persistent seed bank.

Cercidium seed bank. After the first emergence pulse, there were 56 seeds and 40 seedlings in the 30 microsites, for an initial viable seed bank of 96 in 6810 cm², or 141 seeds/m². Fifty-eight percent of the initial viable seed bank remained in the soil. After the second pulse of emergence, the viable seed bank comprised 13 seeds and

TABLE 1. F-STATISTICS AND P-VALUES FROM THE DISCRIMINANT ANALYSIS, SHOWING THE RELATIVE CONTRIBUTION OF TEN CLIMATIC VARIABLES TO EMERGENCE OF *ENCELIA FARINOSA* AND *CERCIDIUM MICROPHYLLUM*. Pre- and post-trigger periods are ±9 or 24 days for *Encelia*, ±3 days for *Cercidium*.

| Variable | Encelia farinosa | | | | Cercidium microphyllum | |
| | ±9 days | | ±24 days | | ±3 days | |
	F	P	F	P	F	P
Pre-trigger rain	1.090	0.313	0.059	0.811	1.312	0.266
Post-trigger rain	1.252	0.281	0.946	0.346	0.096	0.760
Pre-trigger average maximum temperature	0.041	0.842	0.463	0.507	2.577	0.125
Post-trigger average maximum temperature	3.918	0.066	0.283	0.602	1.803	0.195
Pre-trigger average minimum temperature	0.153	0.701	0.190	0.669	7.296	0.014
Post-trigger average minimum temperature	2.558	0.131	0.031	0.863	4.589	0.045
Pre-trigger absolute maximum temperature	0.038	0.848	0.031	0.862	3.101	0.094
Post-trigger absolute maximum temperature	1.201	0.290	0.001	0.980	2.229	0.152
Pre-trigger absolute minimum temperature	0.309	0.586	0.043	0.838	4.667	0.044
Post-trigger absolute minimum temperature	5.832	0.029	0.008	0.931	5.311	0.033

33 seedlings. Twenty-eight percent of the seed bank remained in the soil.

Fouquieria seed bank. No more than a few *Fouquieria* seeds were retrieved from the *Encelia* and *Cercidium* seed bank samples, although adult plants were common in the vicinity and the bright white seeds are relatively large and not easily overlooked. Numerous recently dispersed *Fouquieria* seeds were apparent on the soil surface on June 7, 1993, but by June 15 none was left. Seeds of other woody desert species (e.g., *Ambrosia deltoidea, Encelia farinosa, Larrea tridentata*) were readily visible on the soil at that time. Moreover, although the rainfall requirement for *Fouquieria* emergence was met in 7 of 8 summers, seedlings were sparse and infrequent, suggesting a lack of seed in the soil. Taken together, these circumstances indicate that *Fouquieria* does not have a persistent seed bank.

DISCUSSION

Natural germination requirements. Seeds of desert plants typically do not germinate after small rains, which may be followed by drought (Went 1957). My results suggest that the minimum rain triggers for

emergence are 17 mm for *Cercidium,* 19 mm for *Encelia,* and 25 mm for *Fouquieria.* These values are in accord with emergence triggers reported for *Larrea tridentata* (16 mm) (Went and Westergaard 1949), various Mojave Desert shrubs (25 mm) (Beatley 1974; Ackerman 1979), and *Carnegiea gigantea* (38 mm) (Steenbergh and Lowe 1977). Rainfall triggers presumably operate by raising soil moisture to some threshold value, at which point, given suitable temperatures, imbibition, followed by germination, occurs. In phenological studies such as this one, rainfall amounts are but useful proxies for soil moisture measurements, which often are not available.

Most woody species of the northern Sonoran Desert germinate within a range of temperatures that correspond either to the cool season (October–April) or the warm season (May–September). Natural germination of *Encelia* is restricted to the cool months (Shreve et al. 1937), that of *Cercidium* and *Fouquieria* to the warm ones (Shreve 1917; Shreve et al. 1937). One exception is *Simmondsia chinensis,* which apparently germinates over a wide range of natural temperatures (Sherbrooke 1977). Emergence temperatures seen in this study agree with germination temperatures determined in laboratory studies. The discriminant analyses suggest that, given a large enough rain trigger during the correct season, emergence of *Encelia* and *Cercidium* further depends upon appropriate *minimum* temperatures. *Encelia farinosa* failed to emerge in winters when the absolute minimum temperature during the 9 days after the trigger fell below freezing. On all but one occasion, *Cercidium* emergence failed when average minimum temperatures within 3 days of the trigger fell below 20°C.

Rains sufficient to trigger emergence of *Fouquieria* are not uncommon in the northern Sonoran Desert in summer, yet I observed very few seedlings from 1985–1992. Curiously, Shreve (1917) reported that tens of thousands of the seedlings emerge after early summer rains. He did not specify in which summer he observed *Fouquieria* germination. The discrepancy may be due in part to the timing of summer rains. From 1909–1917, the first summer rains large enough to trigger germination fell on July 4, 1909; July 1, 1911; July 12–13, 1912; July 11, 1916; and July 9, 1917. Between 1985 and 1992, the first triggering rains were generally much later: August 1, 1985; August 30, 1987; August 24, 1988; August 17, 1989; July 15, 1990; August 9, 1991; and July 7, 1992. On Tumamoc Hill, *Fouquieria* disperses seed during May and June. Unless a triggering rain occurs shortly thereafter, most of the seeds are apparently lost from the seed bank. By the time a triggering rain does fall, few or no seeds are left to germinate. It seems likely that Shreve observed

mass emergence in 1909 or 1911, when the first heavy summer rains were rather early.

Fouquieria splendens seed stored at room temperature remains highly viable for 2 years (Mark A. Dimmitt, personal communication). Those few seeds that do remain in the seed bank may well retain viability for several months, and, given a triggering rain during the warm season, should germinate. Thus, I recorded a few *Fouquieria* seedlings on September 11, 1987, October 19, 1989, and August 8, 1990.

Opportunities for germination of woody desert plants vary widely from species to species. Examples include *Agave deserti* (1 of 17 years) and *Ferocactus cylindraceus* (=*Ferocactus acanthodes*) (8 of 18 years) in the northwestern Sonoran Desert (Jordan and Nobel 1979, 1981); *Ambrosia dumosa* (1 of 5 years) and *Larrea tridentata* (1 of 5 years) in the northern Mojave Desert (Ackerman 1979); *Prosopis* sp. (2 of 22 years) in the west-central Sonoran Desert (Turner 1990); and *Cercidium microphyllum* (8 of 9 years) in the northern Sonoran Desert (Shreve 1917). For some of these species, unusual climatic conditions are necessary for germination and emergence. Turner (1990) reported that in MacDougal Crater, Sonora, numerous *Prosopis* seedlings emerged in response to tropical storm Norma (September 1970) and hurricane Joanne (October 1972). In southeastern California, *Agave deserti* germination requires above-normal rains from winter–spring frontal storms (Jordan and Nobel 1979). From 1985 to 1992, suitable conditions for germination and emergence of *Encelia* occurred 8 times on Tumamoc Hill; for *Cercidium,* 13 times; and for *Fouquieria,* 3 times. Of these three species, only *Fouquieria* requires somewhat unusual climatic conditions. Once emergence has occurred, recruitment into the population depends upon favorable climate and escape from predation, a rare combination of circumstances for desert perennial seedlings (Shreve 1917; Sheps 1973; Steenbergh and Lowe 1977; Ackerman 1979; Sherbrooke 1989; McAuliffe 1990).

Emergence events and seed banks of woody desert plants. I observed multiple emergences (two or more in a single season) of *Encelia* and *Cercidium.* Multiple emergences apparently do not exhaust the seed bank of either species. After three emergence pulses, 43 percent of the initial *Encelia* seed bank remained in the soil. After two emergence pulses, 28 percent of the *Cercidium* seed bank was left. Multiple emergence events may reflect age differences in germination requirements. Perhaps the first trigger germinates the oldest seeds, and subsequent triggers bring about germination and emergence of younger cohorts. Alternatively, multiple emergence

events may reflect genetic variability in germination requirements within a single cohort. In either case, different fractions of the seed bank may be responding to different rainfall totals, different soil temperature regimes, or both. Controlled experiments would be necessary to resolve these questions.

Apparently, little is known about the seeds banks of woody dominants in the northern Sonoran Desert (Kemp 1989). Longevity in storage does not necessarily indicate lifespan in the soil. *Carnegiea* and *Larrea* germinated after 7 and 10 years under controlled storage conditions (USDA Forest Service 1974; Valentine and Gerard 1968), and *Fouquieria* retains high viability after 2 years in storage (Mark A. Dimmitt, personal communication). Species known to lack persistent seed banks include *Atriplex canescens* (Kemp 1989), *Carnegiea gigantea* (Steenbergh and Low 1977), and *Larrea tridentata* (Boyd and Brum 1983; Kemp 1989). It seems likely that *Fouquieria* also has a transient seed bank. In fact, the low level of emergence in response to late summer rains suggests that there is little carry-over of seed from the beginning of the summer to the end, much less from year to year. Seeds of *Olneya tesota* require unusually early summer rains to escape heavy predation (Shreve 1951), and it seems possible that the same is true for *Fouquieria*. House finches visit the ripe seed capsules (personal observation); perhaps these and other granivores harvest most of the seed crop as it matures.

Although it has been said that woody plants of warm deserts have minimal dependence on seed banks (Kemp 1989), there are exceptions. Trees and shrubs of the Caesalpinioideae and Mimosoideae often have hard seed coats that prevent germination until the year after dispersal at the earliest (Shreve 1951; Tschirley and Martin 1960; McAuliffe 1990); such species, including *Cercidium* (Shreve 1951) and *Prosopis velutina* (Tschirley and Martin 1960), necessarily have persistent seed banks. *Encelia farinosa* seed also carries over from year to year. For desert annuals, persistent seed banks are widely regarded as a hedge against climatic uncertainty (Wilcott 1974; Venable and Lawlor 1980; Venable 1989). Whether the same is true of woody desert perennials is unknown. Other forces that might select for persistent seed banks in woody desert perennials include phylogenetic constraints (perhaps true of *Cercidium microphyllum* and other woody legumes), early successional life history (perhaps the case for *Encelia farinosa*), and conservation of genetic variability. Clearly, more information on the seed banks and natural germination conditions of woody desert plants is needed before these hypotheses can be tested.

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ANNOUNCEMENT

The Rupert Barneby Award

The New York Botanical Garden is pleased to announce that Dr. André Mauricio de Carvalho, of the Centro de Pesquisas do Cacau, Itabuna, Brasil, and Prof. Ricardo Vanni, of the Instituto de Botánica del Nordeste, Corrientes, Argentina, are the recipients of the **1993 Rupert Barneby Award.** Dr. Carvalho will use his award to continue his work on a taxonomic treatment of New World *Dalbergia*. Prof. Vanni will be able to further his studies of *Zornia* sect. *Anisophylla* in South America, and *Stylosanthes* for the floras of Argentina and Paraguay.

The New York Botanical Garden also invites applications for the **1994 Rupert Barneby Award.** The award of $1,000.00 is to assist researchers planning to come to The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a letter describing the project for which the award is sought, and how the collection at NYBG will benefit their research. Travel to NYBG should be planned between January 1, 1995 and January 31, 1996. The letter should be addressed to Dr. Enrique Forero, Director, Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5156 USA, and received no later than December 2, 1994. Announcement of the recipient will be made by December 16th. Anyone interested in making a contribution to **THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS,** which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Forero.

SCRUB COMMUNITY DESCRIPTIONS OF THE BAJA CALIFORNIA PENINSULA, MEXICO

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ABSTRACT

Qualitative and quantitative data on woody and succulent plant distribution in Baja California, Mexico were collected from 17 January to 21 February, 1991. Qualitative data from 196 samples were then clustered using TWINSPAN, a divisive, polythetic classification program. Fourteen scrub and woodland plant communities are described quantitatively using line-transect data. This is the first quantitative description of scrub plant communities for most of the peninsula. We compared our results with previous classifications and found close agreement in the California Floristic Province of Baja California (northwest). Comparisons were mixed in the Sonoran Desert region, suggesting more complicated mosaic species distributions. In the Sonoran desert, there was a general trend of increasing tree cover correlated with increasing rainfall from north to south. Vegetation maps at 1:250,000 and 1:1,000,000 scales produced in Mexico exist for Baja California. We compared our classification scheme to that used in these maps by first subjectively grouping our samples according to the Mexican scheme. We compared these data with data from the TWINSPAN analysis using indices of similarity. There is little agreement between the two classification schemes. The Mexican scheme, based on dominant life forms, is broader in scope and approximates vegetation types described here only in northern Baja California. Mapping units are poorly defined and there are many inconsistencies among maps. While these maps are a potentially rich source of information, we suggest that they be used only as a general guide to life forms of Baja California.

RESUMEN

Se colectaron datos cuantitativos y cualitativos sobre la distribución de plantas leñosas y suculentas de la Península de Baja California, México, del 17 de enero al 21 de febrero de 1991. Los datos cualitativos, obtenidos de 196 muestras, fueron clasificados mediante el uso del programa TWINSPAN, programa divisivo y polifilético. Para gran parte de la península, ésta es la primera descripción cuantitativa que se realiza. En lo que respecta a la Provincia Florística de California (noroeste de Baja California) los resultados concordaron estrechamente con previas clasificaciones. Sin embargo, en la región del Desierto Sonorense, se obtuvieron concordancias mezcladas por lo que se sugiere la ocurrencia de un mosaico de distribuciones de especies mas complejo. En el Desierto Sonorense se encontró una tendencia general al incremento en cobetura arbórea correlaciorada con el incremento en precipitación pluvial que se observa de norte a sur. Se describe brevemente el esquema de clasificación utilizado en los mapas de vegetación escala 1:250,000 y 1:1,000,000 editados por el gobierno Mexicano. Nuestras muestras fueron clasificadas subjetivamente de acuerdo al esquema Mexicano, y comparadas con los resultados del TWINSPAN utilizando una matriz de similitud. Los resultados de ésta indican poca concordancia entre los dos esquemas de clasificación. El esquema Mexicano, basado en formas de vida

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dominantes, es de escala más amplia y coincide con las comunidades vegetales aquí descritas, sólo en el noroeste de Baja California. Las unidades cartográficas de los mapas no están bien definidas y existen numerosas inconsistencias entre ellos. Sugerimos por tanto que estos mapas sean utilizados solamente como una guía general de las formas de vida vegetales de Baja California.

Vegetation classification and descriptive work in the Baja California peninsula, Mexico (hereafter referred to as Baja California), have been largely qualitative in nature (e.g., Shreve 1951, 1942, 1936; Wiggins 1980, 1969, 1960; Epling and Lewis 1942; Turner and Brown 1982; Hanes 1977; Mooney 1977; Axelrod 1978; Leon de la Luz et al. 1991). The most widely held general classification scheme divides Baja California into eight major plant associations (Wiggins 1980), including the Sonoran Desert communities of Shreve (1951). Turner and Brown (1982), in their treatment of the Sonoran Desert, use the classification scheme of Shreve (1951) and propose numerous types (termed series) within each of the seven Sonoran Desert divisions. Several quantitative vegetation classification studies have been performed in the Californian Floristic Region of Baja California (Westman 1983, 1981; Mooney and Harrison 1972). Quantitative work in the central desert region has been restricted to localized habitat descriptions with line-transect data (Turner and Brown 1982; Humphrey 1974). Plant communities in Baja California Sur north of the Cape region have not yet been studied quantitatively, and no quantitative treatment exists for the peninsula on a large scale.

The main purpose of this study is to provide a quantitative landscape-level classification scheme of perennial vegetation within the scrub communities of most of Baja California. Scrub communities are defined here as lower elevation (generally below 1000 m) vegetation composed primarily of deciduous or evergreen shrubs with total cover not exceeding 90%. Excluded from this work is "hard" chaparral, a dense largely evergreen community common in higher elevations of the Sierra Juarez, Sierra San Pedro Martir and also found in isolated patches in smaller mountain ranges within the Sonoran Desert. Also excluded from this study are scrub communities east of the peninsular range, in the Cape region (S of 24°N), and on the islands in the Gulf of California and the Pacific. These plant communities are well described elsewhere (see Felger and Lowe 1976; Cody et al. 1983; Moran 1983; Arriaga and Leon 1989). The Gulf Islands exhibit very similar plant species composition to the mainland and can even be considered samples of mainland flora and vegetation of comparable area (Cody et al. 1983).

The Mexican government has produced vegetation maps for Baja California at two scales, 1:1,000,000 (Instituto Nacional de Estadistica, Geografia y Informatica [INEGI] 1981) and 1:250,000 (INEGI 1980–1988). Another goal of this paper is to evaluate the accuracy and usefulness in the field of these maps. These maps are extremely

detailed and cover every region of the peninsula, providing a potentially valuable source of information for vegetation scientists. The methodology used to produce these maps, one based on life-form, may not be consistent with more traditional quantitative methods of vegetation analysis. However, vegetation classification based on floristics, such as that presented here, can be highly complementary to that of the structural or life-form classification used in the Mexican maps (Mueller-Dombois and Ellenberg 1974). In order to assess the compatibility between our classification and that for which excellent mapping is available, a direct comparison between the two classification systems is made. Floral nomenclature follows that of Wiggins (1980) except for recent revisions to the genera *Euphorbia* (Huft 1984), *Viguiera* (Schilling 1990), and *Agave* (Gentry 1978). Place names follow INEGI (1978).

Study Site and Methods

In the northwestern region of the peninsula the climate resembles semiarid Mediterranean regions of southern California. Precipitation averages from 130 mm per year at sea level to over 250 mm at 550 m, over 95% of which falls from October to April. Mean January and July temperature is about 12°C and 25°C, respectively (Pase and Brown 1982). South of the peninsular range (30°N) the climate gradually shifts from arid to subtropical, with mean annual precipitation ranging from 50 mm in the north to just over 450 mm in the Cape region. North of the Cape, however, rainfall generally does not exceed 200 mm per year. The western side of the peninsula is generally wetter than the east due to the cooling effect of the California current and the prevalence of coastal fog. On the gulf side and in the southern portion of the peninsula, most rainfall occurs from July to October in the form of tropical storms. Elevations within the study region range from 0–2100 m (the highest mountains are over 3000 m). Soils are generally granitic in origin in the north and volcanic in origin in the south. For a detailed description of the peninsula's complex climate and physiography, see Wiggins (1980), Turner and Brown (1982), Pase and Brown (1982), Roberts (1989) and references therein.

Surveys were performed from 17 January through 21 February, 1991 along 2370 km (1481 mi) of paved and dirt roads as far south as Ciudad Insurgentes (24°N). Transects were located at five-road-mile intervals, on alternating sides of the road. Habitats typical of higher elevation (e.g., dense chaparral dominated by evergreen sclerophyllous shrubs), very low scrub communities (<0.5 m tall), grasslands, or sites with heavy disturbance were not sampled. A few other points were skipped when access was not possible within one mile of the five-mile mark. A total of 196 transects were taken along the survey route.

Vegetation sampling. Floristic composition was determined quantitatively by the use of a 30 meter long line transect following the method of Strong (1966). These began approximately 200 meters from the edge of the disturbed area along the road. Line transects ran perpendicular to the road except when they fell on slopes, in which case they were taken parallel to the slope axis. If the transect fell within a drainage, the transect was taken perpendicular to the drainage. For each transect, the length along the line and maximum width perpendicular to the line of all woody and succulent plants intercepted by the meter tape (with a minimum of 10 cm of material from one plant crossing the line) were recorded. Species density, dominance, frequency, and importance value were then calculated for each transect (Cox 1985). More detailed quantitative measures would have been desirable at each sample area (e.g., Westman 1981; McAuliffe 1990). However, given the time limitations of this survey and the large area over which it had to be performed, the combination of detailed qualitative descriptions and small-scale quantitative data averaged over a larger area were judged to yield the most accurate concept of vegetation patterns.

After the quantitative data were collected, the surveyor began a random walk to record (or collect if unknown; voucher specimens deposited at SDNHM) all perennial woody or succulent species within unaided visual range. At each site, cover estimates (crown diameter) of perennial vegetation were made. We used a modified Daubenmire (1959) cover class for each of four vegetation strata: (1) open space/rock outcrop/herbaceous, (2) small shrubs (<1.5 m tall), (3) large shrubs, and (4) trees. Plant habit rather than height distinguished the latter classes, as many short-statured trees are present in desert vegetation. The most conspicuous species in each of these layers were recorded as dominants (maximum of four) along with all other perennial species present that could be located within 30–40 minutes. In almost all cases, this was adequate time to identify all but the rarest woody and succulent species.

Vegetation classification. Each sample was first classified subjectively using the qualitative information found on Mexican vegetation maps (INEGI 1980–1988). These plant associations were then grouped into 12 higher level vegetation types and compared to vegetation types of the independent computer analysis with a matrix of similarity. Computer classification was based on data from the qualitative surveys only. Dominant species of each strata were given a score of two and all other species present were give a score of one. This gave equal weight to dominant species of different vegetation strata, regardless of their relative cover or abundance. Classification was based on species composition of the different strata rather than their absolute or relative abundances. Thus, each stratum was rep-

resented, even if it comprised a small portion (in terms of dominance and/or density) of the vegetation type. This equal weighting may more accurately distinguish important structural vegetation differences. For example, in many desert plant communities in Baja California, trees are uncommon in the landscape and would be a small part of any total cover value. However, they probably represent a disproportionately more important component (e.g., as avian habitat). However, in some cases, this asymmetric weighting may place excessive emphasis on rare but visually conspicuous species (e.g. *Pachycereus pringlei, Stenocereus thurberi, Idria columnaris*).

Classifications were based on the results of TWINSPAN (Two-Way Indicator Species Analysis), a polythetic, divisive classification scheme that uses the technique of reciprocal averaging to ordinate stands, producing a hierarchical tree (Hill 1979; Gauch 1982; Causton 1988). Classifications were based on a weighting of four to one for "conspicuous" versus "present" species. Absolute plant abundances were omitted from the TWINSPAN classification in favor of two abundance classes because a comparison of qualitative and quantitative data indicated that open cover was consistently underestimated in the qualitative surveys. This does not necessarily result in a loss of information. Given the degree of variation inherent in most species' spatial distribution, detailed measurements on species abundance for the purposes of large scale classification are usually unnecessary (Gauch 1982). Nine outlier transects were eliminated from this analysis. These included transects that fell in small drainages which were later pooled with adjacent more widespread vegetation type. Once the vegetation classification was determined, data from line transects were grouped accordingly. Species densities, dominance and frequency were averaged within vegetation types to arrive at a quantitative estimate of vegetation composition. Due to the small amount of quantitative sampling within each vegetation type (one 30-meter transect every five miles), the quantitative results should be used only as a guide. Indicator species were determined from TWINSPAN output with refinements based on quantitative results. Twenty-one plants that could not be identified to the species level were omitted from indicator status. Vegetation types were compared using a matrix of similarity.

RESULTS

Vegetation classification. A total of fourteen scrub communities are described in this paper. The final dendrogram, including characteristic species ("indicator species") and dominants for these TWINSPAN classifications, are shown in Figure 1. Indicator species are not necessarily the dominant or most common species in the

FIGURE 1. CLASSIFICATION DENDROGRAM. Hierarchical tree produced by TWIN-SPAN. Sample sizes, vegetation type indicator and dominant species are also included. See text for explanation of indicator species.
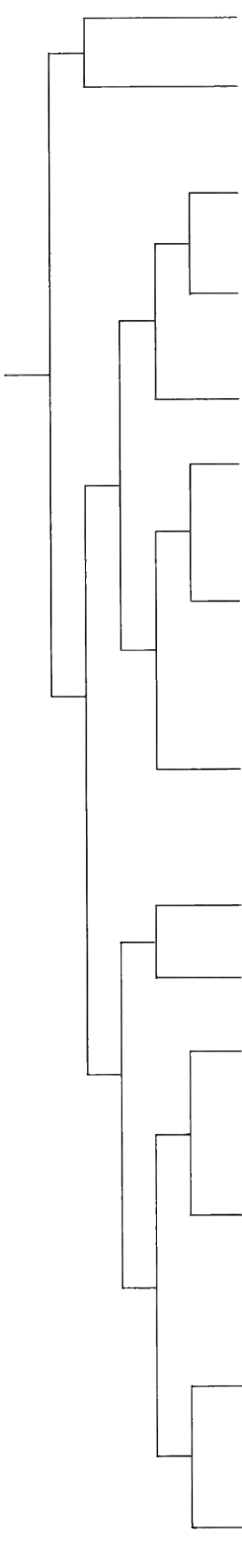
Dendrogram	Habitat type	Sample points	Indicator species
	Diegan coastal sage scrub	23	*Artemisia californica, Viguiera laciniata, Malosma laurina*
	Martirian coastal succulent scrub	15	*Stenocereus gummosus, Agave shawii* ssp. *shawii, Ambrosia chenopodifolia*
	Central Vizcainan mixed scrub	17	*Stenocereus gummosus, Opuntia cholla, Pedilanthus macrocarpus, Idria columnaris*
	Sonoran creosote-bursage scrub	22	*Ambrosia magdalenae, A. dumosa, Opuntia echinocarpa, Idria columnaris*
	Vizcaino Plain desert scrub	5	*Encelia halimifolium*
	Rosarian coastal mixed scrub	6	*Agave shawii* ssp. *shawii, Stenocereus gummosus, Euphorbia misera, Frankenia palmeri, Ambrosia chenopodifolia, Idria columnaris*
	Northern Vizcaino Plain mixed scrub	4	*Agave shawii* ssp. *goldmaniana, Euphorbia misera, Frankenia palmeri, Ambrosia chenopodifolia, Idria columnaris, Pachycormus discolor*
	Vizcainan foothill desert scrub	7	*Atriplex julacea, Fouquieria diguetii, Agave shawii* ssp. *goldmaniana, Idria columnaris, Pachycormus discolor*
	Inland Gulf coast desert scrub	10	*Stenocereus thurberi, Jatropha cinerea, J. cuneata*
	Magdalenan coastal dune scrub	22	*Asclepias masonii, Lophocereus schottii, Jatropha cinerea*
	Central Gulf coast desert scrub	24	*Jatropha cuneata, Cercidium microphyllum, Bursera microphylla, Pedilanthus macrocarpus, Larrea tridentata, Stenocereus thurberi*
	Southern Gulf coast desert scrub	17	*Jatropha cuneta, Cercidium microphyllum, Lysiloma candida, Bursera microphylla, Ruellia californica, Olneya tesota, Stenocereus thurberi*
	Basaltic desert woodland	9	*Jatropha cuneata, Cercidium praecox, Prosopis palmeri, Euphorbia californica, Stenocereus thurberi*
	Basaltic desert scrub	6	*Jatropha cuneata, Cercidium praecox, Acacia brandegeana, Stenocereus thurberi*

FIGURE 1. EXTENDED.

Dominant species

Eriogonum fasciculatum, Viguiera laciniata, Artemisia californica, Salvia munzii

Rosa minutifolia, Ambrosia chenopodifolia, Agave shawii shawii, Euphorbia misera

Ambrosia chenopodifolia, Eriogonum fasciculatum, Larrea tridentata, Opuntia cholla, Fouquieria splendens

Larrea tridentata, Ambrosia chenopodifolia, Ambrosia dumosa

Encelia halimifolium, Larrea tridentata, Prosopis glandulosa var. *torreyana, Lycium bierlandei, Stenocereus gummosus*
Euphorbia misera, Agave shawii shawii, Ambrosia chenopodifolia, Atriplex polycarpa, Frankenia palmeri

Frankenia palmeri, Bursera microphylla, Ambrosia chenopodifolia, Euphorbia misera, Agave shawii goldmaniana

Lycium sp., *Fouquieria diguetii, Agave shawii goldmaniana, Euphorbia misera, Atriplex julacea*

Larrea tridentata, Ambrosia deltoides, Opuntia cholla, Stenocereus gummosus, Fouquieria diguetii
Lycium sp., *Fouquieria diguetii, Stenocereus gummosus, Jatropha cinerea, Larrea tridentata, Opuntia cholla*
Jatropha cuneata, Fouquieria diguetii, Ambrosia bryantii, Ambrosia camphorata

Jatropha cuneata, Bursera microphylla, Fouquieria diguetii, Ruellia peninsularis, Ruellia californica, Cercidium microphyllum, Lysiloma candida

Prosopis palmeri, Jatropha cuneata, Lycium sp., *Cercidium praecox, Opuntia cholla*

Jatropha cuneata, Fouquieria diguetii, Bursera microphylla, Larrea tridentata, Opuntia cholla

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vegetation type. However, the presence of at least two of these in-dicators, plus the habitat's overall geographical extent, should be sufficient to distinguish the vegetation types in the field as they are defined here. Because many of the vegetation types are distinguish-able from location alone, the indicator species listed are meant to aid in the differentiation of types that occur in close proximity. A comparison of species composition among the vegetation types is shown in Table 1. The location of sample sites supporting these vegetation types are shown in Figures 2 and 3. In the interest of space, only dominance values for 187 perennial species encountered are present here (Appendix 1).

Californian region. Two widespread scrub communities are pres-ent in this coastal region. The northernmost, Diegan coastal sage scrub (DCSS) (sensu Westman 1983), is characterized by the pres-ence of two small shrubs, the drought-deciduous *Artemisia califor-nica* and the evergreen *Viguiera laciniata,* and one larger shrub, *Malosma laurina.* Total cover is approximately 50%. This vegeta-tion type is found along the coast from the international border just south of San Vincente at elevations up to 640 m (2100 ft.).

Martirian coastal succulent scrub (MCSS) (sensu Westman 1983) is found from just north of Colonet along the coast to San Quintín. This vegetation type is also present east of El Rosario and this area may be contiguous with MCSS along the coast via inland areas not surveyed. This type differs markedly from DCSS in that succulent species have a higher dominance and species richness. The most common of these are *Agave shawii* ssp. *shawii, Euphorbia misera,* the prostrate cylindrical cactus *Stenocereus gummosus,* and the tree-like cactus *Myrtillocactus cochal. Rosa minutifolia,* a small densely-branched spiny shrub, sometimes grows in almost pure stands within this vegetation type. This vegetation type has the largest total dom-inance of any scrub community in this analysis (54.2%).

Sonoran Desert. Between San Quintín and El Rosario is Rosarian coastal mixed scrub (RCMS), a vegetation type that appears tran-sitional between the Californian region to the north and the Sonoran desert to the south and east. This type is allied more closely (albeit weakly) with the Sonoran desert vegetation types and is characterized by the presence of elements of both communities (see Appendix 1). Largely Sonoran Desert species such as *Idria columnaris* and *Opun-tia cholla* also become common in this vegetation type.

Ten vegetation types in this study clearly lie within the boundaries of the Sonoran Desert (including RCMS). The two southernmost types may or may not be part of the Sonoran desert region and are discussed later. Two of the northernmost types, Central Vizcainan mixed scrub (CVMS) and Sonoran creosote-bursage scrub (SCBS), occupy the central highlands region between approximately 30°N
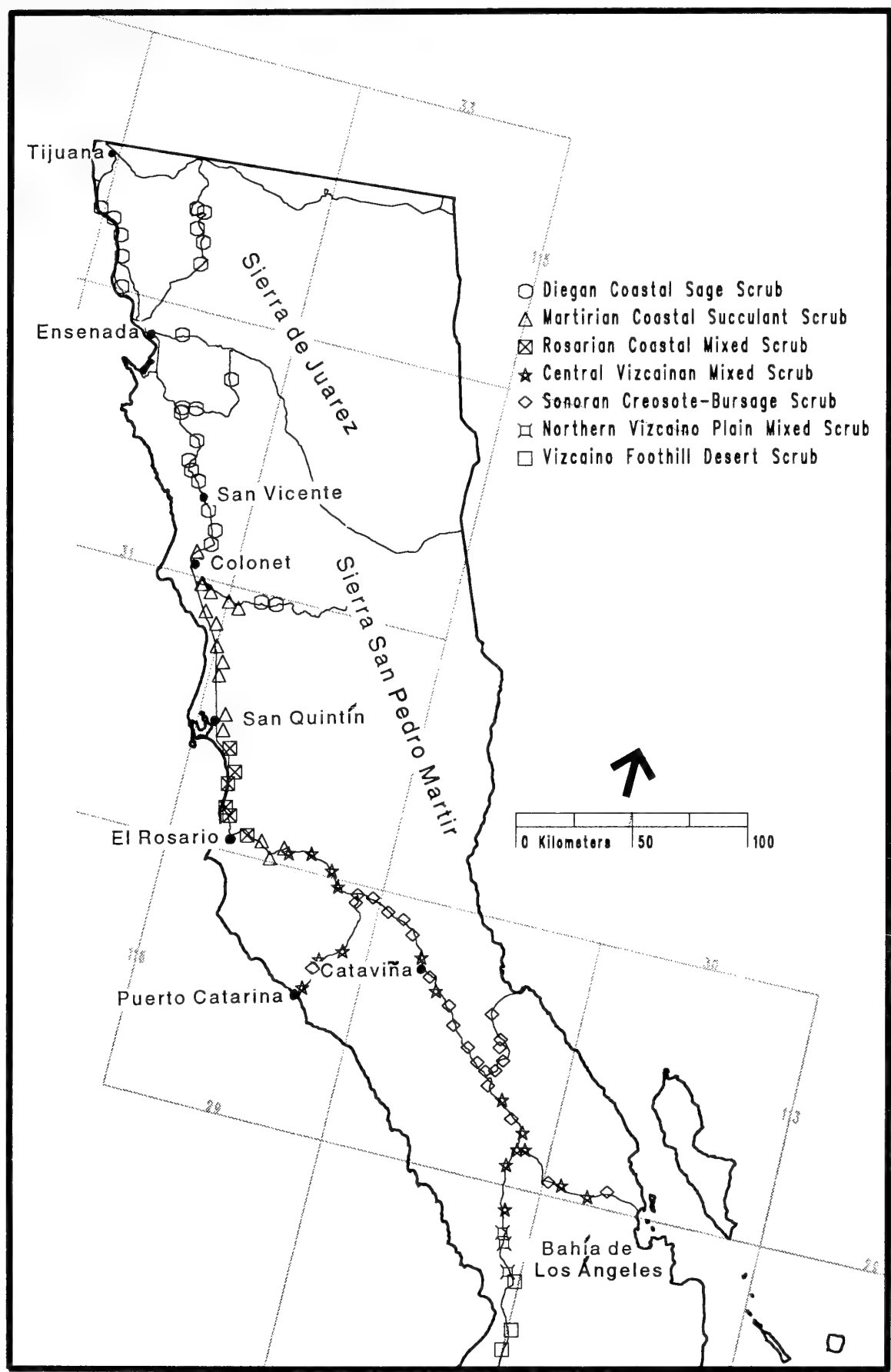
FIG. 2. Transect locations and vegetation types for Baja California. Names of places and topographical features mentioned in the text are also given.
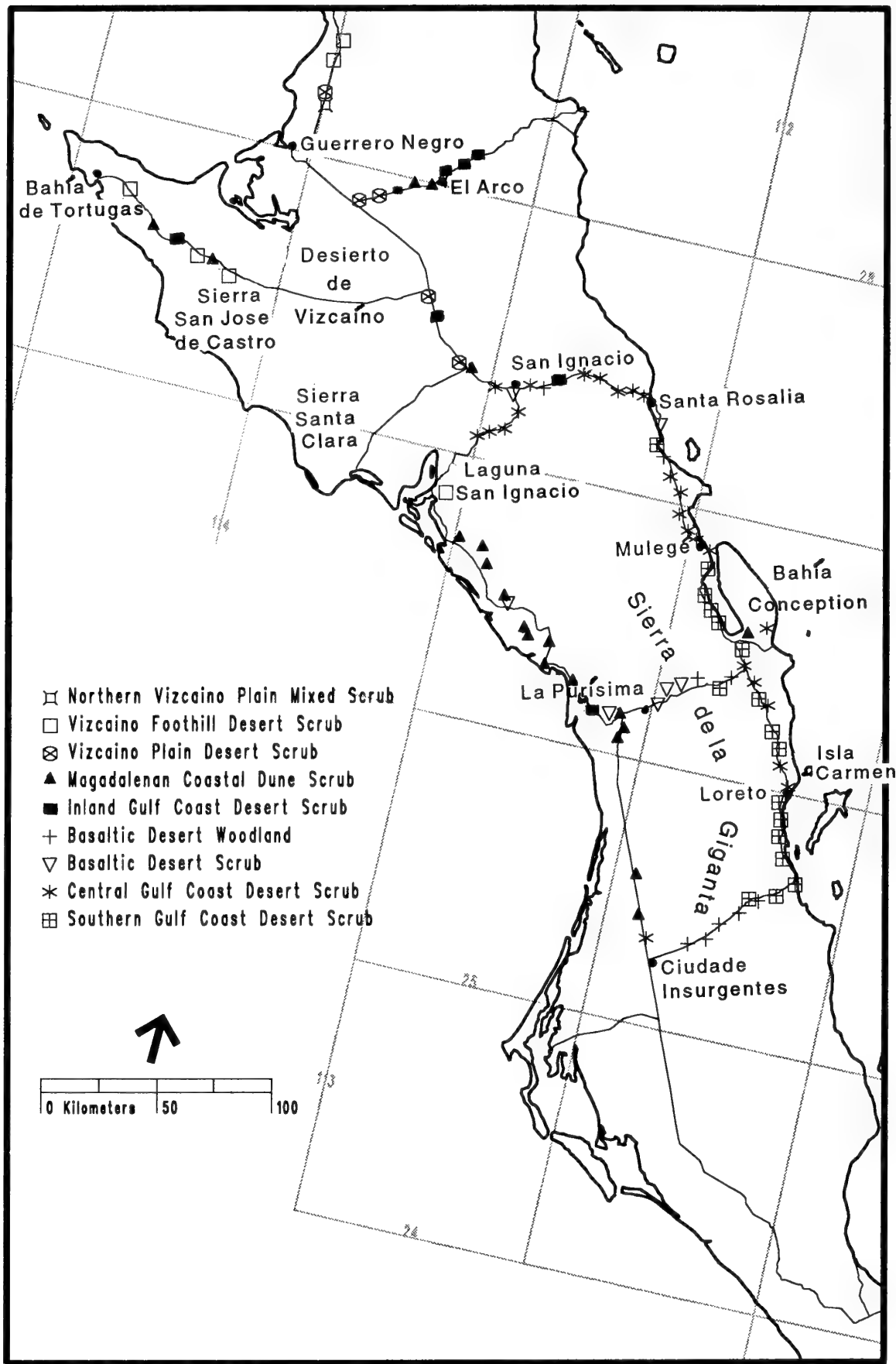
Fig. 3. Transect locations and vegetation types for Baja California Sur. Names of places and topographical features mentioned in the text are also given.

TABLE 1. Comparison Among Vegetation Types. Values are similarity indices calculated from the equation (2C/A + B)·100, where C is the number of species in common to both vegetation types and A and B are the total number of species present in each type, respectively (Sørensen 1948). Values are slight overestimates of similarity because 21 genera representing plants not identified to the species level were also used (e.g., *Lycium* sp.)

	DCSS	MCSS	CVMS	SCBS	VPDS	RCMS	NVPMS	VFDS	IGCDS	MCDS	BDS	BDW	CGCDS
MCSS	63.5												
CVMS	17.9	45.4											
SCBS	31.5	40.4	66.7										
VPDS	12.2	25.6	39.2	41.5									
RCMS	41.0	58.2	34.7	28.9	38.6								
NVPMS	17.3	28.6	50.0	37.0	47.3	32.1							
VFDS	7.1	22.5	38.4	35.7	55.2	30.5	49.1						
IGCDS	10.4	19.8	40.0	40.0	42.7	22.2	38.6	52.8					
MCDS	23.8	26.7	50.0	51.4	45.8	28.6	41.5	56.5	67.2				
BDS	10.9	20.4	28.0	26.1	39.4	23.9	33.8	35.3	40.4	40.9			
BDW	8.2	15.0	30.4	37.1	33.8	16.7	22.9	30.1	51.9	53.6	61.7		
CGCDS	15.5	21.4	45.8	48.3	48.9	19.8	36.0	28.3	68.3	59.8	23.0	59.8	
SGCDS	11.0	11.4	35.5	31.2	33.7	11.9	17.1	25.9	46.6	45.4	38.7	61.2	59.8

and 29°N in a mosaic distribution. Species composition and total dominance of these two vegetation types are very similar. Their distinction lies mainly in species abundance (Appendix 1). CVMS is dominated more by small shrubs. SCBS includes the region around Cataviña, in which large granitic boulders are abundant. Unique indicator species for SCBS include *Ambrosia magdalenae, A. dumosa,* and *Opuntia echinocarpa.* Also noteworthy is that the conspicuous large spiny shrub, *Fouquieria diguetii,* is present in CVMS and not in SCBS.

Several low mountain ranges within the Vizcaíno Desert, including the Sierra Santa Clara, the Sierra Morro Hermosa, and the Sierra San Jose de Castro, form the only major topographic relief of the area and harbor distinct vegetation types from the surrounding sea of very low scrub (not sampled). Vizcaíno Plain desert scrub (VPDS) is found in the low-lying areas along Highway 1 with fine sandy soil and scattered small dunes. This vegetation type is most closely allied with the Sonoran Desert scrub communities to the north (CVMS, SCBS) due to the dominance of *Larrea tridentata* and *Stenocereus gummosus.* Distinction in the field, however, is based on the presence of *Encelia halimifolium,* which has the highest dominance in that vegetation type. Vizcaíno foothill desert scrub (VFDS) is found north of Guerrero Negro at slightly higher elevations (>50 m) in more mixed soil types and on the Vizcaíno peninsula in the foothills of the Sierra Morro Hermoso and the Sierra El Placer. A single location is also found just south of Laguna San Ignacio along the coast. *Bursera microphylla,* one of the dominant species, is most common on the peninsular mountains, while the *Agave shawii* ssp. *goldmaniana* is most common north of the Guerrero Negro. VFDS has the lowest dominance of any of the communities in this analysis (23.1%). Also aligned closely with VFDS is Northern Vizcaíno Plain mixed scrub (NVPMS), which is found in the vicinity of Rosarito and north of Guerrero Negro. It can be distinguished from VFDS by the presence of *Ambrosia chenopodiifolia* and *Frankenia palmeri,* and the absence of *Atriplex julacea.* This vegetation type is closely allied compositionally, but not geographically, with RCMS due to the sharing of several dominant widespread small shrubs (e.g., *Ambrosia chenopodiifolia, Euphorbia misera,* and *F. palmeri*). Due to the relatively small sample sizes for these three types (Fig. 1), their complete distribution within the Vizcaíno Plain is unknown. Tree and shrub species richness reach their lowest point for the study area in the Vizcaíno Desert.

The six remaining communities are largely restricted to the Magdalena Plain and gulf coast regions south of 28°N and are compositionally closely allied. The two northernmost of these communities, Inland Gulf coast desert scrub (IGCDS) and Magdalenan coastal dune scrub (MCDS) are distinguished from the other four primarily

by the rarity or complete absence of *Jatropha cuneata,* a drought-deciduous shrub that becomes very abundant south of 27.5°N. IGCDS is generally found in the Vizcaíno Plain eastern foothills and inland gulf valleys, both with sandy soils. MCDS is found mostly in the sandy soils along the Pacific coast southeast of Laguna San Ignacio. This vegetation type occupies the narrow (about 10 km) fringe between the coast and the mesas to the east. In addition, several locations were found to the north: two in the Vizcaíno peninsular foothills, two in the El Arco region and one near Bahía de los Ángeles. The far northern sample lacks any small shrub cover and may represent an anomaly. However, the other three samples clearly represent communities closely allied with the Pacific coast communities.

The four remaining vegetation types are all characterized by the abundance of one species, *J. cuneata,* which is the most dominant in three of the four communities (and second in the fourth). Large legume trees such as *Cercidium microphyllum, C. praecox, Prosopis palmeri,* and *Lysiloma candida* become common. Total plant cover increases to values seen in the Californian region (40–50%). Central Gulf coast desert scrub (CGCDS) and Southern Gulf coast desert scrub (SGCDS) are found generally in the coastal outwash plains (bajadas) of the Sierra de la Giganta along the Gulf coast. The former is also found inland west of Santa Rosalía. SGCDS is dominated primarily by *J. cuneata* but has sixteen species with dominance values of 1% or greater. *Lysiloma candida* is common in this vegetation type, especially in drainages, and helps differentiate the southern GCDS from the central GCDS.

The last two communities are found primarily in the higher elevations (up to 350 m) in basaltically-derived soils, sometimes amidst large basaltic boulders. Basaltic desert scrub (BDS) is found at least between Highway One and La Purísima with some additional samples west of Santa Rosalía. Basaltic desert woodland (BDW) farther south is characterized by the dominant presence of *P. palmeri* (15.2%), covering almost twice the area of *J. cuneata* in BDW or BDS, hence the term "woodland." This vegetation type is found primarily in the western foothills of the Sierra de la Giganta northeast of Ciudad Insurgentes, with some samples scattered farther north.

Mexican vegetation classification. The results of the subjective classification based on the INEGI vegetation types done prior to the computer analysis are compared with the results of this study in a similarity matrix (Table 2). In northwest Baja California, the INEGI vegetation types are more general than those presented here. DCSS appears to fit well within the bounds of one INEGI vegetation type, *chaparral-vegetación secudaria arbustiva. Matorral rosetófilo costero* overlaps with two vegetation types, MCSS and RCMS. These are

TABLE 2. COMPARISON BETWEEN OUR CLASSIFICATION, BASED ON SPECIES PRESENCE/ABSENCE, AND THE MEXICAN CLASSIFICATON, BASED ON DOMINANT LIFE FORMS. Similarity coefficients are calculated in the same way as in Table 1. Mat. = Matorral; Veg. = Vegetación.

Classification—this study	Classification—Mexican scheme											
	Mat. rosetófilo costero	Chaparral-veg. secudaria arbustiva	Veg. halófila	Mat. desértico rosetófilo	Mat. sarco-crasicaule	Mat. desértico micrófilo	Veg. de desiertos arenosos	Mat. sarco-crasicaule de neblina	Mezquital	Mat. sarcocaule	Mat. sarco-caule Cardonal	Mat. sarco-caule-subinerme
DCSS	12	91	0	0	0	0	0	0	0	0	0	0
MCSS	75	0	0	0	0	0	0	0	0	0	0	0
RCMS	38	0	0	0	0	0	0	0	0	0	0	0
CVMS	6	0	0	25	65	0	0	0	0	0	0	0
SCBS	0	0	0	26	26	59	0	0	0	0	5	0
VPDS	0	0	0	0	0	25	22	0	0	0	0	0
NVPMS	0	0	0	0	24	0	25	0	0	0	0	0
VFDS	0	0	17	0	7	0	36	0	0	42	0	0
CGCDS	0	0	0	0	0	0	0	6	0	0	25	57
SGCDS	0	0	0	0	0	0	0	0	27	0	24	33
MCDS	0	0	30	0	0	10	0	40	0	15	19	11
IGCDS	0	0	0	0	0	14	0	11	0	24	19	7
BDS	0	0	0	0	0	0	0	0	0	0	15	22
BDW	0	0	0	0	0	0	0	0	29	0	29	7

the only close equivalents in terms of species presence. The other vegetation types presented here resemble portions of two to five other INEGI communities. Most vegetation types share few or no species with those of the Mexican classification.

DISCUSSION

Californian region. Westman (1983) identified three plant communities in north coastal Baja California (Table 3) using an analysis very similar to that presented here. Diegan coastal sage scrub is the southernmost coastal sage scrub association along the Pacific coast of North America and is dominated by mesophyllous, seasonally dimorphic and drought-deciduous species. It also has the highest species richness per sample area of all of the coastal central and southern Californian region scrub communities (Westman 1983). Results from this study generally support these two classifications of Westman (1983), including their geographical extent. However, quantitative results differ. For DCSS, our analysis revealed a strong dominance by *Viguiera laciniata,* only encountered rarely by Westman. The reason for this is likely Westman's small sample size (n = 3) in this vegetation type. The dominant and uncommon species listed for the Martirian coastal succulent scrub community by Westman differed significantly from our results. The two most dominant species in our analysis were listed in Westman (1983) as present in only a minority of samples. In addition, his dominants have relatively low dominance in our study. This may indicate that, while this vegetation type is easily distinguishable from surrounding types, it is very heterogeneous in species composition on a local scale. We found that several species (many of which are listed as rare or endangered in the United States) were much more common across the border in the Diegan coastal sage scrub that we surveyed. These included *Rosa minutifolia, Salvia munzii,* and *Euphorbia misera.* However, while these species were sometimes dominants, they were absent from many of our samples. Thus, our results support those of Westman (1983), who did not make a distinction between vegetation types across the border.

The boundary between the Californian region and the Sonoran Desert cannot be drawn by a single line on a map due to the transitional nature (ecotone) of the vegetation in this region (Shreve 1951; Turner and Brown 1982; Wiggins 1980). El Rosario has traditionally been the cutoff between the two major floristic regions and floristic support for this division is not lacking. Many important components of the Sonoran Desert reach their northwestern limits at or near El Rosario, including *Fouquieria splendens, Idria columnaris, Larrea tridentata,* and *Agave cerulata* (Shreve 1951; Hastings et al. 1972; Gentry 1978). However, there are many other species

TABLE 3. A COMPARISON OF VEGETATION TYPES BETWEEN THIS AND PREVIOUS STUDIES ON BAJA CALIFORNIA.

This study	Shreve (1951) and Wiggins (1980)	Turner and Brown (1982)	Westman (1983)
Diegan coastal sage scrub	Californian Region		Diegan coastal sage scrub
Martirian coastal succulent scrub			Martirian coastal succulent scrub
Central Vizcainan mixed scrub		Vizcaino Subdivision (in part)	Vizcainan coastal succulent scrub
Sonoran creosote-bursage scrub			
Vizcaino Plain desert scrub			
Rosarian coastal mixed scrub	Sarcophyllous Desert (in part)	Maguey-Boojum Series	
Northern Vizcaino Plain mixed scrub		Frankenia-Ocotillo-Datilillo Series	
Vizcainan foothill desert scrub			
Inland Gulf coast desert scrub	Sarcocaulescent Desert (in part)	Central Gulf Coast Subdivision (in part)	
Central Gulf coast desert scrub		Torchwood-Cardon Series	
Southern Gulf coast desert scrub			
Magdalenan coastal dune scrub	Magdalenan Region (in part)	Magdalena Plain Subdivision (in part)	
Basaltic desert woodland	Sierra de la Giganta Region (in part)	Cape Region (in part)	
Basaltic desert scrub			

whose range overlaps the two regions significantly. More conspicuous ones include *Eriogonum fasciculatum, Simmondsia chinensis, V. laciniata, Euphorbia misera, Agave shawii* ssp. *shawii,* and *Ambrosia chenopodifolia* (Shreve 1951; Hastings et al. 1972; Gentry 1978).

Westman (1983) identifies a scrub community surrounding El Rosario that is distinct from the Martirian community to the north, termed Vizcainan coastal succulent scrub. He groups this association within the Californian region, although he acknowledges the possibility of a closer affinity with the Sonoran Desert. Our results confirm Westman's speculations of an affinity (albeit weak) of this association with the vegetation of the Sonoran desert, renamed Rosarian coastal mixed scrub (RCMS) in order to distinguish this from the Vizcaíno desert plant communities farther south. Figure 4 shows our slightly modified boundaries of the Californian region, as well as other modifications of the major Sonoran desert subdivision discussed later. The ultimate fate of RCMS is largely moot as it clearly represents a broad ecotone between the Sonoran desert and Californian region. It is worth noting the inclusion by Westman (1983) of *Amblyopappus pusillus* (Asteraceae), a spring-blooming annual, as the dominant species of this vegetation type. Our study did not correspond to the flowering time of this species. However, it is surprising that one annual species could so dominate the landscape of this area, which Westman states is characterized by relatively high shrub dominance (41.65%) and diversity. Our sample size within this region is only n = 6, as is Westman's (1983). This may account for some of the discrepancies in species composition.

Sonoran Desert. In the seminal work on Sonoran Desert flora, Shreve (1951) identified seven distinct floristic regions, four of which occur in Baja California. These divisions were made based solely on qualitative vegetation characteristics, although they generally correspond to physiographic and climatic regions as well (Shreve 1951; Turner and Brown 1982). This general mapping was later modified by Brown and Lowe (1980) and included in Turner and Brown (1982). The TWINSPAN classification presented here gives a large-scale pattern of Sonoran Desert plant communities generally similar to that proposed by Shreve (1951), with several notable deviations discussed below.

The microphyllous desert (syn. Lower Colorado River Valley subdivision) extends into the region of this survey only at its southern tip in a narrow band along the gulf coast as far south as Bahía de los Ángeles. Sonoran creosote-bursage scrub (SCBS) is the only vegetation type described here that would fit well in this category, with its dominance by *Larrea tridentata* and *Ambrosia* spp. However, comparison with qualitative descriptions (Shreve 1951; Turner and
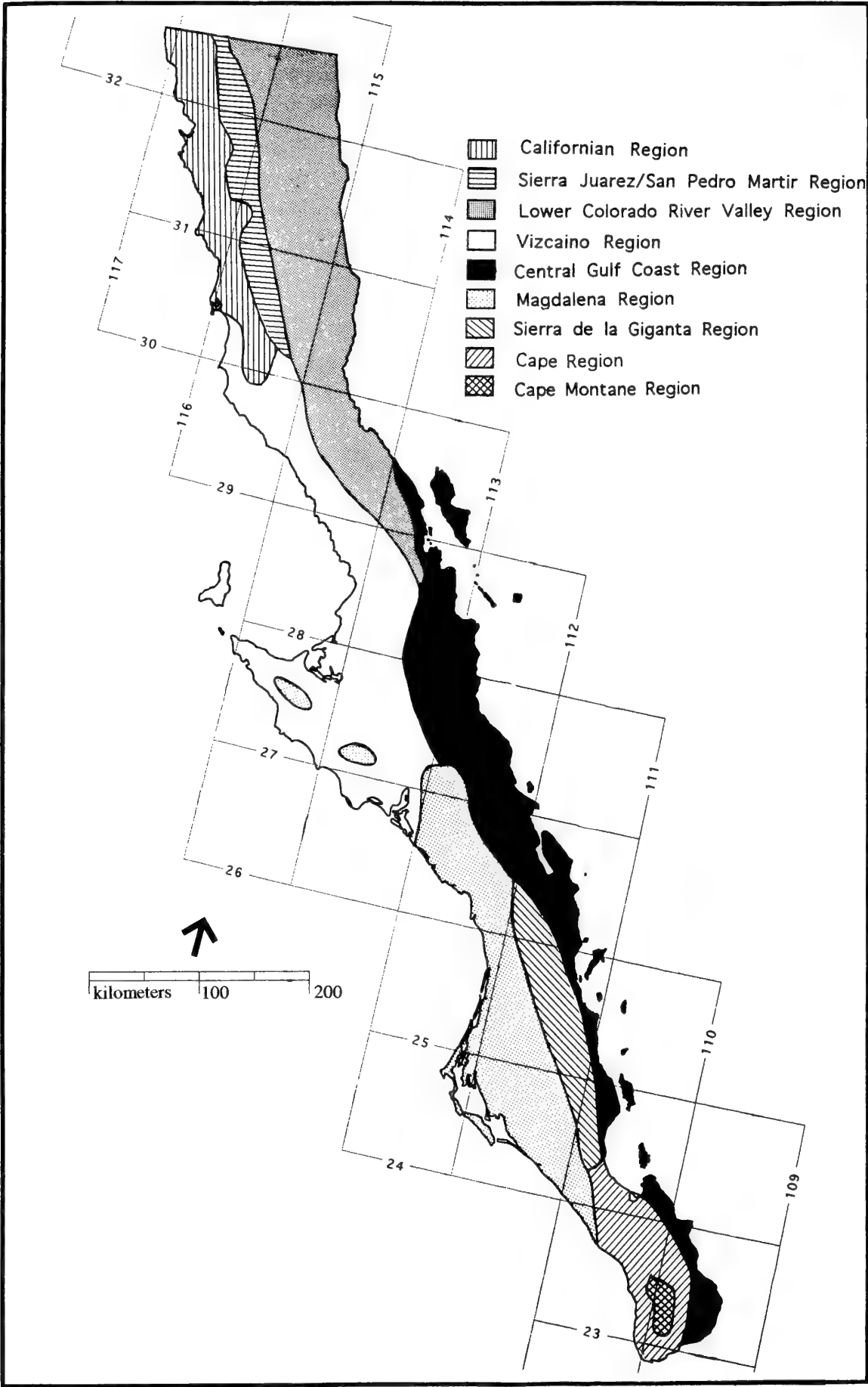
Fig. 4. Baja California general plant community distribution (modified from Wiggins 1980 and Turner and Brown 1983).

Brown 1982) shows a much higher shrub diversity present in SCBS. The southern end of this subdivision is not well described, so a detailed comparison is not possible. According to this analysis, the southern limits of this subdivision could be moved farther inland than currently recognized, to encompass more of the central highlands surrounding Highway One. Closely allied samples cross the boundaries of the remaining three divisions, sarcophyllous desert (syn. Vizcaíno subdivision), sarcocaulescent desert (syn. Central Gulf Coast subdivision) and Magdalenan, although the majority are restricted to the individual regions.

Our analysis reveals a complex pattern of vegetation in the Vizcaíno Desert mountains (the Sierra Santa Clara is mapped as a similar complex mosaic of Sonoran Desert vegetation types by Leon de la Luz 1991). This may be due in part to their isolation from the more inland mountains. In addition, however, mean summer temperatures are at least 5°C lower than that of other Sonoran Desert regions, largely due to the coastal fog influence of the Pacific Ocean (Turner and Brown 1982). The vegetation of the flat desert plain is primarily composed of two vegetation types, neither of which were sampled in this study. The first is dominated by very low (<0.5 m) shrubs of mostly *Frankenia palmeri* and *Atriplex* spp., especially *A. julacea* (Turner and Brown 1982; Leon de la luz et al. 1991). The second is found on stabilized and unstabilized dune fields throughout the peninsula. Vegetation in these areas is composed of a wider diversity of life forms (shrubs include *Larrea tridentata, Lycium californicum, Errazurizia megacarpa* and *Atriplex barclayana*), although it is still relatively species-depauperate (Leon de la Luz et al. 1991).

The sarcocaulescent desert is described for Baja California along the Gulf coast in a coastal strip about 40 km wide from 29.5°N to almost the tip of the peninsula. Turner and Brown (1982) add to Shreve's description that "There is a general absence of a low shrub cover layer. . . ." Our data do not support this statement, at least on the Baja peninsula region of this subdivision (it extends along a similar coastal region in Sonora); shrub cover along the coast (CGCDS and SGCDS) is comparable to that of other Sonoran desert communities (15–25% cover). Average annual rainfall in this subdivision varies widely, from 71 mm in the north (Bahía de los Ángeles), to 270 mm in the south (Turner and Brown 1982), with a mean of 134.8 mm (SD = 55.2). Turner and Brown analyzed rainfall data from Baja California and Sonora within this subdivision and found only a weak correlation between latitude and rainfall amount. We analyzed rainfall data from only the Baja California side of the Sea of Cortez (n = 12) and found a strong correlation with latitude (corr. coeff. = −0.769); no correlation exists between elevation and rainfall patterns. This gradual increase in rainfall as one moves south along

the Gulf coast would suggest an equally gradual transition in vegetation along the same area. This is supported at least as far as 25.5°N latitude. Central Gulf coast desert scrub gives way to Southern Gulf coast desert scrub farther south. Moreover, there is a clear trend towards greater tree cover moving south along the entire study route.

It appears that IGCDS is a transitional vegetation between the sarcocaulescent desert and the Magdalenan region, and could actually be placed in either (although the TWINSPAN analysis allies this vegetation type with MCDS). If it is placed in the former subdivision as is proposed here (Fig. 4), the boundaries of the sarcocaulescent desert would be moved farther inland to at least the vicinity of El Arco (28°N, 113.5°W).

Turner and Brown (1982) built on the general classification scheme of Shreve (1951), classifying many localized plant communities (termed "series"; Table 1). Within these series, visual dominants were qualitatively identified. They performed a intensive quantitative survey near Punta Prieta using thirty 30.5 m long line transects (R. Turner personal communication 1991), describing the localized agave-boojum series. Because the samples of this and of our study were taken on different scales, comparison is unwarranted. However, it is worth noting that *Fagonia californica* had the highest density recorded for any species in their samples, but a very low dominance (0.74%; relative dominance = 0.03%) (Turner and Brown 1982). An effort was made to locate this species, a prostate-spreading perennial herb (Zygophyllaceae), in this vicinity during our survey, but very few individuals were found. *Eriogonum fasciculatum* was present in the Punta Prieta area in abundance, yet none were recorded in the transects of Turner and Brown (1982). This may represent a change in vegetation patterns between the times of the two surveys.

Turner and Brown (1982) also sampled the Cataviña area quantitatively and described the Ragged-leaf goldeneye–boojum series, a localized community associated with distinctive abundant granitic outcrops. Our analysis failed to separate this localized vegetation type, even at more detailed TWINSPAN classifications (past those described here). This could possibly be due to our small sample size in this vegetation type (n = 5). However, it is more likely that the species composition around Cataviña is not significantly distinct from the adjacent regions and does not merit a separate vegetation type based on composition alone.

Scant attention has been paid to the Pacific coastal region between San Ignacio and the Cape region by phytogeographers, and although boundaries have been drawn by various workers (Shreve 1951; Shreve and Wiggins 1964; Turner and Brown 1982), a detailed description is lacking. This study describes one vegetation type within the northern portion of this region, Magdalenan coastal dune scrub, of which three samples extend beyond its recognized northern boundaries.

This may further illustrate the very gradual transitions of vegetation patterns seen throughout Baja California.

Subtropical Cape region. In Shreve (1951) and most other subsequent treatments of Baja California Sonoran Desert vegetation, the boundary between the subtropical Cape region and the Sonoran Desert traces a triangle approximately between Comondú, La Paz and Todos Santos. Thus the Cape region is usually defined as below 24°N except for a 20 kilometer-wide belt stretching northwest up to 26.5°N, essentially encompassing the Sierra de la Giganta range up to Bahía Concepción. This boundary dates back to at least 1911 (see refs in Shreve and Wiggins [1964], p. 10). In contrast, our analysis shows little compositional difference between the two communities (BDS and BDW) occurring within Shreve's subtropical Cape region and those within the Sonoran Desert proper. Another worker has noted similar discrepancies (Leon de la Luz personal communication 1991). These boundaries, according to Shreve, were defined purely on the basis of vegetation and flora: "The vegetation of the Sonoran desert is distinguished from that of adjacent regions by the wide differences in appearance between dominant plants" (Shreve and Wiggins 1964, p. 39). Even though BDW has a much higher cover of thorny trees than any other vegetation type (over 20%), Shreve's statement leads one to expect greater compositional differences. However, there were relatively few samples in this area and no comparison was made with regions farther south that are clearly part of the Cape region. Wiggins (1980) proposed two general regions within the subtropical Cape Region, the Sierra de la Giganta Region and the Arid Tropical Region. Our analysis would support this boundary between the vegetation of the northern finger of the subtropical region and the very distinct vegetation of the Cape. However, the question of whether the vegetation of the Sierra de la Giganta would be considered part of the Sonoran Desert remains unanswered.

Mexican vegetation classification and mapping. There are advantages to using a life-form classification scheme in relatively open, desert habitats. For one, aerial photography can be used to map large areas using this classification method (Goldsmith 1974). In addition, this method can be useful for large-scale comparisons both within a region and across ecosystems (Kent and Coker 1992). However, the almost completely subjective nature of life-form classification often raises questions about the repeatability of the methods. Those unfamiliar with the vegetation of the region may find such a classification difficult to interpret in the field (Kent and Coker 1992). Classification based on floristic data is also appropriate for desert ecosystems due to the relative ease in identification of the perennial component of the vegetation. Baja California is unique among Mex-

ican regions in that an excellent flora is available (Wiggins 1980), thus allowing a detailed, repeatable classification method such as that presented here.

There are sixteen vegetation types listed on the Mexican maps for the region within this survey. Many are further split into several associations and a list of dominant and conspicuous species within variable strata categories is included with almost every map. Classification was based on the dominant life form of a given area and was determined by subjective visual analysis (Vargas-Medoza personal communication 1991) using aerial photography and field verification (INEGI 1980–1988) in conjunction with the previous work of Miranda and Hernandez X. (1968) and Rzedowski (1978). However, the classification method is not explicitly defined and we were unable to find a published account of the methods.

Given the different goals of the two classification methods, it is not surprising that the comparison of vegetation types (Table 2) showed little similarity. Most vegetation types appear to share no common species. This is partially due to the short list of species given for the Mexican types. Because this list includes both dominants (as defined in this paper) and visually conspicuous species, we could not limit our list of species in a similar manner. While DCSS appears to fit within the bounds of one INEGI vegetation type, *chaparral–vegetación secudaria arbustiva,* it extends far beyond the elevational range of Diegan coastal sage scrub and probably includes other commonly recognized scrub communities such as those dominated by *Artemisia tridentata* or *Arctostaphylos* spp. (D. Zippin personal observation).

There are several major inconsistencies between the 1:1,000,000 scale and 1:250,000 scale Mexican vegetation maps, particularly for chaparral, *vegetación halófilo,* and *vegetación sarcocaule.* While qualitative descriptions are given for dozens of localized plant communities, few are mapped at either of the 1:1,000,000 and 1:250,000 scales. A revision of the 1:1,000,000 scale map has been completed for the Vizcaíno Biosphere Reserve (located between 28°N and 26.5°N from coast to coast, including the entire Vizcaíno Desert; Leon de la Luz et al. 1991). This revision has corrected much of the inaccuracy in the *vegetación halófilo* community. However, many inconsistencies between the two maps remain, which call into question the accuracy of the 1:250,000 scale maps. In regions most similar in vegetation to that of the United States, we found the use of these maps particularly difficult. Mapping units were clearly defined quite differently from those across the border. Efforts are currently underway to standardize vegetation sampling and classification across California. If international cooperation in vegetation management and protection is to occur, compatible definitions must be agreed upon for the vegetation types that our counties share. In conclusion,

the Mexican classification does not correspond well to the vegetation classification presented in this study. The life form classification scheme used in these maps may be useful to vegetation scientists in some instances. However, the mapping of these life form associations should be used only as a general guide, perhaps only at the 1:1,000,000 scale.

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APPENDIX 1. DOMINANCE VALUES FOR PLANT COMMUNITIES. Species are grouped according to their closest vegetation affinities (i.e., associations within and among sample stands). General life forms: C = columnar succulent; S = succulent; Sb = subshrub; Sh = shrub; T = tree. Plant community types: DCSS = Diegan coastal sage scrub; MCSS = Sonoran creosote–bursage scrub; VPDS = Vizcaino Plain desert scrub; RCMS = Rosarian coastal mixed scrub; NVPMS = Northern Vizcaino Plain mixed scrub; VFDS = Vizcaino foothill desert scrub; IGCDS = Inland Gulf Coast desert scrub; MCDS = Magdalenan coastal dune scrub; BDS = Basaltic desert scrub; BDW = Basaltic desert woodland; CGCDS = Central Gulf Coast desert scrub; SGCDS = Southern Gulf Coast desert scrub. P = species present in vegetation type but not recorded by line transect.

Species	Family	General life form	Plant community		
			DCSS	MCSS	CVMS
Ambrosia camphorata	Asteraceae	Sb	—	—	0.40
Aeschynomene nivea	Fabaceae	Sh	—	—	—
Berginia virgata var. *glandulifera*	Acanthaceae	Sh	—	—	—
Bourreria sonorae	Boraginaceae	Sh	—	—	—
Bursera epinnata	Burseraceae	T	—	—	—
Caesalpinia placida	Fabaceae	Sh	—	—	—
Castela polyandra	Simaroubaceae	Sh	—	—	—
Cercidium microphyllum	Fabaceae	T	—	—	—
Cochemia poselgeri	Cactaceae	S	—	—	—
Colubrina viridis	Rhamnaceae	Sh	—	—	—
Cordia parvifolia	Boraginaceae	Sh	—	—	—
Euphorbia sp.	Euphorbiaceae	Sh	—	—	—
Hoffmanseggia intricata	Fabaceae	Sh	—	—	—
Hyptis anitae	Lamiaceae	Sh	—	—	—
Krameria paucifolia	Krameriaceae	Sh	—	—	—
Lysiloma candida	Fabaceae	T	—	—	—
Olneya tesota	Fabaceae	T	—	—	—
Passiflora foetida var. *longipedunculata*	Passifloraceae	Sh	—	—	—
Pithecellobium confine	Fabaceae	Sh	—	—	—
Ruellia californica	Acanthaceae	Sh	—	—	—
Bursera microphylla	Burseraceae	T	—	—	0.40
Jatropha cuneata	Euphorbiaceae	Sh	—	—	—
Bursera odorata	Burseraceae	T	—	—	—
Krameria parvifolia var. *parvifolia*	Krameriaceae	Sh	—	—	—
Stenocereus thruberi	Cactaceae	S	—	—	—
Acacia brandegeana	Fabaceae	T	—	—	—
Agave aurea	Agavaceae	S	—	—	—
Bursera cerasifolia	Burseraceae	T	—	—	—
Bursera filifolia	Burseraceae	T	—	—	—
Cercidium praecox	Fabaceae	T	—	—	—
Desmanthus covellei	Fabaceae	Sh	—	—	—
Echinocereus brandeegei	Cactaceae	S	—	—	—
Prosopis palmeri	Fabaceae	T	—	—	—
Ruellia cordata	Acanthaceae	Sh	—	—	—
Ruellia peninsularis	Acanthaceae	Sh	—	—	—

APPENDIX 1. EXTENDED.

| | | | | | Plant community | | | | | |
SCBS	VPDS	RCMS	NVPMS	VFDS	IGCDS	MCDS	BDS	BDW	CGCDS	SGCDS
0.13	—	—	—	—	—	—	4.81	1.38	P	—
—	—	—	—	—	—	—	—	—	P	0.64
—	—	—	—	—	—	—	—	P	—	0.62
—	—	—	—	—	—	—	—	—	—	0.07
—	—	—	—	—	P	—	—	—	0.20	0.79
—	—	—	—	—	P	—	—	—	0.07	1.52
P	—	—	—	—	—	—	—	—	P	—
—	—	—	—	—	0.30	P	—	P	1.13	2.62
—	—	—	—	—	—	—	—	P	0.18	P
—	—	—	—	—	P	—	—	0.93	0.25	2.13
—	—	—	—	—	—	—	—	0.29	0.88	1.79
—	—	—	—	—	—	—	—	—	P	—
—	—	—	—	—	—	—	—	—	—	0.24
—	—	—	—	—	—	—	—	—	—	0.80
—	—	—	—	—	—	—	0.99	—	0.17	0.70
—	—	—	—	—	—	—	P	P	P	2.54
P	—	—	—	—	P	P	—	0.08	P	1.77
—	—	—	—	—	—	—	—	—	—	P
—	—	—	—	—	—	—	—	—	0.49	—
—	—	—	—	—	—	—	—	0.66	0.14	2.97
P	—	—	4.89	2.15	1.70	1.20	1.45	0.85	6.07	4.13
—	—	—	—	—	1.32	P	9.04	9.24	11.52	9.28
—	—	—	—	—	—	—	—	P	—	P
—	P	—	—	—	—	—	0.91	P	0.30	P
—	—	—	—	—	0.21	P	0.11	0.55	0.16	1.49
—	—	—	—	—	—	—	2.61	—	—	—
—	—	—	—	—	—	—	P	—	—	—
—	—	—	—	—	—	—	—	P	—	—
—	—	—	—	—	—	—	P	—	—	—
—	—	—	—	—	—	—	2.87	6.29	—	0.36
—	—	—	—	—	—	—	1.51	P	—	—
—	—	—	—	P	0.26	0.09	1.27	0.19	0.18	—
—	—	—	—	—	—	—	P	15.17	—	—
—	—	—	—	—	—	—	0.33	—	—	—
—	—	—	—	—	P	—	P	1.56	—	3.52

Appendix 1. Continued.

Species	Family	General life form	Plant community		
			DCSS	MCSS	CVMS
Bursera hindsiana	Burseraceae	T	—	—	—
Agave sp.	Agavaceae	S	—	—	—
Ambrosia bryantii	Asteraceae	Sh	—	—	—
Ferocactus diguetii	Cactaceae	S	—	—	0.18
Fouquieria diguetii	Fouquieriaceae	Sh	—	—	0.40
Opuntia ciribe	Cactaceae	S	—	—	—
Cercidium sp.	Fabaceae	T	—	—	—
Echinocereus engelmannii	Cactaceae	S	—	—	—
Ephedra sp.	Ephedraceae	Sh	—	—	—
Jatropha cinerea	Euphorbiaceae	Sh	—	—	P
Sapium biloculare	Euphorbiaceae	Sh	—	—	—
Ephedra trifurca	Ephedraceae	Sh	—	P	—
Euphorbia magdalenae	Euphorbiaceae	Sh	—	—	—
Fagonia californica	Zygophyllaceae	Sb	—	—	P
Hyptis sp.	Lamiaceae	Sh	—	—	—
Lippia palmeri	Verbenaceae	Sb	—	—	—
Lycium bierlandei	Solanaceae	Sh	—	—	—
Lycium californicum	Solanaceae	Sh	—	—	1.29
Opuntia sp.	Cactaceae	S	—	—	—
Opuntia tapona	Cactaceae	S	—	—	—
Phaulothamnus spinescens	Phytolaccaceae	Sh	—	—	—
Ruellia sp.	Acanthaceae	Sh	—	—	—
Trixis angustifolia	Asteraceae	Sh	—	—	—
Viguiera deltoidea	Asteraceae	Sh	—	—	—
Asclepias masonii	Asclepiadaceae	Sh	—	—	—
Condalia globosa	Rhamnaceae	Sh	—	—	—
Jacquemontia abutiloides	Convolvulaceae	Sb	—	—	—
Maytenus phyllanthoides	Celastraceae	Sh	—	—	—
Suaeda sp.	Chenopodiaceae	Sb	—	—	—
Opuntia cholla	Cactaeae	S	0.07	0.31	1.96
Prosopis sp.	Fabaceae	T	P	—	0.29
Ambrosia deltoides	Asteraceae	Sh	—	—	—
Euphorbia californica	Euphorbiaceae	Sh	—	—	0.50
Euphorbia xantii	Euphorbiaceae	Sh	—	—	P
Pedilanthus macrocarpus	Euphorbiaceae	Sh	—	—	0.07
Bebbia juncea	Asteraceae	Sh	—	—	—
Euphorbia tomentulosum	Euphorbiaceae	Sh	—	—	P
Lophocereus schottii	Cactaceae	C	0.85	—	0.69
Pachycereus pringlei	Cactaceae	C	—	P	0.40
Solanum hindsianum	Solanaceae	Sh	—	—	P
Ambrosia magdalenae	Asteraceae	Sh	—	—	—
Calliandra californica	Fabaceae	Sh	—	—	—
Hymenoclea sp.	Asteraceae	Sh	—	—	—
Lycium sp.	Solanaceae	Sh	0.22	0.51	1.56
Viguiera microphylla	Asteraceae	Sh	—	—	—
Larrea tridentata	Zygophyllaceae	Sh	—	—	2.06
Ditaxis lanceolata	Euphorbiaceae	Sb	—	—	—
Encelia farinosa	Asteraceae	Sh	—	—	—
Prosopis articulata	Fabaceae	T	—	—	0.12

APPENDIX 1. EXTENDED. CONTINUED.

				Plant community						
SCBS	VPDS	RCMS	NVPMS	VFDS	IGCDS	MCDS	BDS	BDW	CGCDS	SGCDS
—	—	—	—	P	1.08	P	—	P	0.18	0.62
—	—	—	—	—	0.40	—	P	—	—	—
—	—	—	—	0.63	1.06	0.12	6.63	1.24	P	—
0.11	—	—	—	—	—	—	—	—	—	—
—	0.48	—	1.29	3.54	6.11	2.35	6.69	2.39	6.92	3.55
—	1.55	—	—	—	—	1.12	1.05	0.04	0.40	P
—	—	—	—	—	—	P	—	—	—	—
—	—	—	—	—	—	—	0.25	0.29	0.21	P
0.76	—	0.79	—	—	—	P	—	—	—	—
P	1.03	—	—	P	3.89	1.03	P	0.79	1.00	2.40
—	—	—	—	—	P	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	P
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	P
—	—	—	—	—	0.15	—	—	—	—	P
—	2.69	—	—	—	—	—	—	—	—	—
—	—	—	1.63	—	—	—	—	—	—	P
P	—	P	—	—	P	P	P	—	—	—
—	—	—	—	—	—	—	P	—	—	—
—	—	—	—	—	P	P	—	—	—	—
—	—	—	—	—	0.08	—	—	—	—	—
—	—	—	—	—	P	—	—	—	—	—
—	—	—	—	—	P	P	—	—	—	P
—	—	—	—	—	—	P	—	—	—	—
—	—	—	—	—	0.34	—	—	—	—	—
—	—	—	—	—	—	P	—	—	—	P
—	—	—	—	—	0.25	0.49	—	—	—	—
—	—	—	—	—	0.30	—	—	—	—	—
0.13	1.28	P	P	—	2.31	2.56	1.86	3.11	2.21	2.43
0.14	—	—	—	—	—	—	—	—	0.33	2.34
—	—	—	—	P	0.29	3.13	—	P	0.30	—
P	—	—	—	—	0.09	1.00	—	2.23	0.41	0.67
—	—	—	P	—	0.07	—	P	—	P	P
—	0.58	—	—	—	0.40	0.71	—	0.19	0.36	P
0.08	—	—	—	—	—	—	—	—	—	P
—	—	—	—	—	—	0.38	—	—	—	0.08
0.33	P	P	—	P	—	0.65	—	—	0.23	0.24
0.11	P	P	—	P	0.13	0.16	0.16	0.13	0.02	P
0.78	P	—	P	—	0.15	1.27	P	0.20	P	0.20
1.03	P	—	—	P	P	1.64	—	—	0.25	P
0.11	—	—	—	P	P	—	—	—	P	—
P	—	—	—	—	—	—	—	—	—	—
0.75	1.28	1.88	—	4.43	6.26	1.60	2.83	7.85	1.18	1.82
—	—	—	—	—	P	—	—	—	0.35	—
9.08	5.47	—	0.33	P	2.79	6.07	P	P	4.53	0.53
—	—	—	—	—	—	—	—	—	—	0.10
0.64	—	—	—	—	P	0.32	—	P	P	P
0.20	—	—	—	—	—	—	—	—	—	—

APPENDIX 1. CONTINUED.

Species	Family	General life form	Plant community		
			DCSS	MCSS	CVMS
Viguiera purisimae	Asteraceae	Sh	—	—	—
Errazurizia benthamii	Fabaceae	Sh	—	—	—
Frankenia palmeri	Frankeniaceae	Sh	—	—	—
Encelia halimifolia	Asteraceae	Sh	—	—	0.30
Ferocactus peninsulae	Cactaceae	S	—	—	P
Yucca valida	Agavaceae	S	—	—	0.49
Acacia farnesiana	Fabaceae	T	—	—	—
Acacia greggii	Fabaceae	Sh	—	—	P
Acanthogilia gloriosa	Polemoniaceae	Sh	—	—	P
Ambrosia dumosa	Asteraceae	Sh	—	0.39	0.03
Asclepias albicans	Asclepiadaceae	Sh	—	—	—
Bursera sp.	Burseraceae	T	—	—	P
Dalea spinosa	Fabaceae	Sh	—	—	P
Fouquieria splendens	Fouquieriaceae	Sh	—	—	1.90
Haplopappus sonorensis	Asteraceae	Sh	—	—	—
Krameria grayi	Krameriaceae	Sh	—	—	—
Lycium andersonii	Solanaceae	Sh	—	1.14	—
Lycium exsertum	Solanaceae	Sh	—	—	0.13
Mammilaria sp.	Cactaceae	S	P	0.02	P
Prosopis glandulosa var. torreyana	Fabaceae	T	—	—	0.36
Yucca schidigera	Agavaceae	S	—	—	P
Agave cerulata	Agavaceae	S	—	—	0.48
Beloperone californica	Acanthaceae	Sh	—	—	P
Opuntia molesta	Cactaceae	S	—	—	0.71
Opuntia tesajo	Cactaceae	S	—	—	0.20
Vizcainoa geniculata	Zygophyllaceae	Sh	—	—	P
Atriplex barclayana	Chenopodiaceae	Sh	—	—	P
Atriplex julacea	Chenopodiaceae	Sh	—	—	0.38
Encelia sp.	Asteraceae	Sh	—	—	0.25
Haplopappus venetus	Asteraceae	Sh	—	—	—
Pachycormus discolor	Anacardiaceae	T	—	—	1.05
Atriplex sp.	Chenopodiaceae	Sh	—	0.47	0.51
Encelia californica	Asteraceae	Sh	P	0.66	0.71
Idria columnaris	Fouquieriaceae	C	—	0.12	1.08
Atriplex canescens	Chenopodiaceae	Sh	—	P	—
Opuntia acanthocarpa	Cactaceae	S	0.06	—	P
Stenocereus gummosus	Cactaceae	S	—	2.41	0.54
Viguiera triangularis	Asteraceae	Sh	—	0.23	0.67
Ferocactus acanthodes	Cactaceae	S	—	P	P
Ferocactus sp.	Cactaceae	S	—	0.03	—
Agave shawii ssp. goldmaniana	Agavaceae	S	—	—	—
Ambrosia divaricata	Asteraceae	Sh	—	—	—
Atriplex polycarpa	Chenopodiaceae	Sh	—	—	0.08
Mirabilis laevis	Nyctaginaceae	Sh	P	0.10	P
Opuntia echinocarpa	Cactaceae	S	P	—	P
Opuntia ramosissima	Cactaceae	S	P	0.19	0.40
Acalypha californica	Euphorbiaceae	Sh	P	P	P

APPENDIX 1. EXTENDED. CONTINUED.

				Plant community						
SCBS	VPDS	RCMS	NVPMS	VFDS	IGCDS	MCDS	BDS	BDW	CGCDS	SGCDS
P	—	—	—	—	0.57	0.53	P	P	—	—
—	—	—	—	0.29	—	0.10	—	—	0.21	—
—	P	3.78	6.23	0.41	0.42	P	—	—	0.21	—
0.54	8.49	—	—	0.86	P	0.37	—	—	P	0.05
P	—	—	P	P	P	—	—	—	P	—
0.30	0.83	—	P	0.23	P	P	—	—	P	—
—	—	—	—	—	P	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
2.85	—	—	—	—	—	—	—	—	—	—
P	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	0.30
—	—	—	—	—	—	—	—	—	—	—
1.22	—	—	—	—	—	—	—	—	—	—
—	P	—	—	—	—	—	—	—	—	—
0.17	—	—	—	—	—	—	—	—	—	—
—	—	0.37	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
P	P	0.47	P	—	P	P	P	P	0.01	—
0.35	4.93	—	—	—	—	—	—	—	—	—
P	—	—	—	—	—	—	—	—	—	—
0.66	—	—	—	P	0.13	1.51	—	—	0.18	—
—	—	—	—	—	—	—	—	—	—	P
0.29	—	—	—	—	0.07	1.42	—	0.15	P	—
0.45	—	—	P	—	—	0.16	0.82	0.30	—	—
—	—	—	—	—	P	0.35	—	—	P	—
—	—	—	P	—	—	—	0.45	—	—	—
—	—	—	0.08	2.23	—	—	—	—	P	—
—	P	—	P	0.89	P	0.19	—	—	P	—
—	—	P	—	—	—	—	—	—	—	—
—	—	—	2.54	1.40	P	P	—	—	—	—
0.07	P	2.05	0.17	1.58	1.49	—	—	—	0.05	—
0.03	—	—	—	—	1.35	0.43	—	—	—	—
0.31	—	—	P	P	—	P	—	—	—	—
—	P	—	—	P	0.16	—	0.19	—	P	—
0.19	—	—	—	—	0.30	P	—	0.40	0.54	0.40
P	2.57	0.71	0.77	0.16	4.32	2.57	0.38	1.86	1.57	2.46
—	—	—	—	—	—	—	—	—	P	1.00
0.03	0.22	—	P	P	P	—	—	—	0.04	—
—	P	P	—	P	—	0.27	0.32	—	—	—
—	—	—	3.56	2.41	—	—	—	—	—	—
—	—	—	—	—	0.09	—	—	—	0.05	—
0.51	P	5.92	—	—	—	—	—	—	—	—
—	—	—	—	—	—	P	—	—	—	P
0.04	—	—	—	—	—	—	—	—	—	—
P	—	0.09	—	—	—	—	—	—	—	—
0.52	0.07	—	—	—	—	—	—	—	P	—

APPENDIX 1. CONTINUED.

Species	Family	General life form	DCSS	MCSS	CVMS
Hyptis tephrodes	Lamiaceae	Sh	—	—	—
Lycium torreyi	Solanaceae	Sh	—	2.47	1.27
Yucca whipplei	Agavaceae	S	P	0.43	P
Ambrosia chenopodiifolia	Asteraceae	Sh	0.47	10.37	7.09
Opuntia prolifera	Cactaceae	S	—	P	P
Agave shawii ssp. shawii	Agavaceae	S	P	6.40	1.49
Dudleya edulis	Crassulaceae	S	P	0.05	—
Echinocereus maritimus	Cactaceae	S	—	0.09	—
Echinocereus sp.	Cactaceae	S	—	—	—
Euphorbia misera	Euphorbiaceae	Sh	0.52	3.98	1.08
Acacia sp.	Fabaceae	T	—	—	P
Cleome isomeris	Capparaceae	Sh	P	P	P
Eriogonum fasciculatum	Polygonaceae	Sh	13.66	1.37	4.63
Simmondsia chinensis	Buxaceae	Sh	1.33	2.57	0.25
Malacothamnus sp.	Malvaceae	Sh	P	—	—
Viguiera laciniata					
Adolphia californica	Asteraceae	Sh	10.74	1.22	0.23
Ambrosia ambrosioides	Rhamnaceae	Sh	P	—	—
Baccharis glutinosa	Asteraceae	Sh	—	—	P
Haplopappus berberidis	Asteraceae	Sh	P	—	—
Haplopappus propinquus	Asteraceae	Sh	P	—	—
Juniperus californica	Cupressaceae	T	P	—	—
Prunus fremontii	Rosaceae	Sh	1.90	—	P
Rhamnus crocea	Rhamnaceae	Sh	0.21	—	—
Rhus ovata	Anacardiaceae	Sh	P	—	—
Artemisia californica	Asteraceae	Sh	8.43	1.09	—
Asclepias subulata	Asclepiadaceae	Sh	0.08	—	—
Dudleya pulverulenta	Crassulaceae	S	P	—	—
Eriodictyon sessifolium	Hydrophyllaceae	Sh	0.24	—	—
Ferocactus viridescens	Cactaceae	S	P	—	—
Fraxinus trifoliata	Oleaceae	Sh	0.12	—	—
Keckiella antirrhinoides	Scrophulariaceae	Sh	P	—	—
Opuntia parryi var. parryi	Cactaceae	S	P	—	—
Ribes indicorum	Grossulariaceae	Sh	P	—	—
Sambucus mexicana	Caprifoliaceae	Sh	P	—	—
Baccharis sarothroides	Asteraceae	Sh	P	P	—
Cneoridium dumosum	Rutaceae	Sh	1.04	0.18	—
Malosma laurina	Anacardiaceae	Sh	1.57	0.55	P
Rhus integrifolia	Anacardiaceae	Sh	1.02	P	—
Salvia apiana	Lamiaceae	Sh	0.37	P	—
Salvia munzii	Lamiaceae	Sh	6.90	1.98	—
Ephedra californica	Ephedraceae	Sh	0.13	P	—
Aesculus parryi	Aesculaceae	Sh	1.36	0.37	—
Haplopappus linearifolius	Asteraceae	Sh	0.13	0.26	—
Bergerocactus emoryi	Cactaceae	S	1.75	0.34	—
Rosa minutifolia	Rosaceae	Sh	0.70	12.62	—
Trixis californica	Asteraceae	Sh	0.28	P	—
Dudleya sp.	Crassulaceae	S	P	0.11	P

APPENDIX 1.   EXTENDED. CONTINUED.

| Plant community | | | | | | | | | | |
SCBS	VPDS	RCMS	NVPMS	VFDS	IGCDS	MCDS	BDS	BDW	CGCDS	SGCDS
0.37	—	—	—	—	—	—	—	—	—	—
P	—	—	—	—	—	—	—	0.32	—	—
P	—	—	P	—	—	—	—	—	—	—
7.03	—	6.62	4.17	—	—	0.17	—	—	—	—
P	—	P	—	—	—	—	—	—	—	—
—	—	7.11	—	—	—	—	—	—	—	—
—	—	0.26	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	P	0.28	0.11	—	0.08	P	—	—	—	—
—	—	12.58	3.98	2.30	0.57	0.16	0.27	—	0.12	—
—	—	—	—	—	—	0.95	—	—	—	—
—	—	P	—	—	—	—	—	—	—	—
1.02	—	—	—	—	—	—	—	—	—	—
P	—	—	P	—	—	P	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
1.46	—	—	—	—	—	0.52	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	P	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	1.43	0.37	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	P	—	—	—	—	—	—	—	—
—	—	P	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
P	—	—	—	—	—	—	—	—	—	—
—	—	0.09	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	2.30	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
P	—	—	—	—	—	0.27	—	—	P	—
—	—	1.18	0.27	—	—	—	—	—	—	—

APPENDIX 1. CONTINUED.

Species	Family	General life form	Plant community		
			DCSS	MCSS	CVMS
Myrtillocactus cochal	Cactaceae	S, T	P	1.37	P
Opuntia littoralis	Cactaceae	S	0.13	P	—
Adenostoma fasciculatum	Rosaceae	Sh	0.06	P	—
Atriplex lentiformis	Chenopodiaceae	Sh	—	0.81	—
Ceanothus verrucosus	Rhamnaceae	Sh	—	P	—
Galvezia juncea var. *juncea*	Scrophulariaceae	Sh	—	—	—
Quercus dumosa	Fagaceae	Sh	—	P	—
Lycium brevipes	Solanaceae	Sh	—	1.40	—
Boulders			0.34	0.50	0.55
Unknown woody plants			0.89	0.69	1.99
Bareground/herbaceous			48.70	45.19	63.21

APPENDIX 1. EXTENDED. CONTINUED.

					Plant community					
SCBS	VPDS	RCMS	NVPMS	VFDS	IGCDS	MCDS	BDS	BDW	CGCDS	SGCDS
—	—	P	—	—	—	—	P	—	—	—
—	—	P	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	P	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	P	—	—	0.86	—	—	0.30	—	—
2.69	—	—	—	—	—	—	—	—	—	—
2.06	0.91	—	1.46	2.59	0.79	0.86	1.58	3.10	0.70	0.64
65.81	70.96	58.35	66.21	76.86	59.38	65.81	59.31	50.85	61.45	50.63

A HETEROSTYLOUS *GILIA* (POLEMONIACEAE) FROM CENTRAL NEVADA

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Abstract

Gilia heterostyla occurs in deep alluvial sands on floors and lower slopes of north–south valleys of northern Nye County in central Nevada. It is morphologically similar to *G. nyensis, G. subacaulis,* and *G. hutchinsifolia* differing from these species by its distylous flowers, as well as several floral and leaf features. It is the first member of the Polemoniaceae found to be heterostylous.

An attractive, magenta-flowered annual *Gilia* (Polemoniaceae) from southern Nevada was noted in the early 1960's by Janice Beatley during her ecological studies at the Atomic Energy Commission Test Site in Nye County (now the Department of Energy Nevada Test Site). The conspicuous, many-branched plants, with abundant flowers and exserted stamens, were found growing in deep white sand at the base of volcanic tuff outcrops. Numerous collections were made, many by James Reveal, who described the species as *Gilia nyensis* (Reveal 1969).

During subsequent surveys of the Test Site and adjacent regions with William Rhoads and Michael Williams during the late 1970's, the first author observed and collected specimens of a *Gilia* that appeared morphologically similar to *G. nyensis,* but with longer, paler corollas. Closer examination revealed that the plants were distylous. Within a population some individuals had flowers with long styles and short stamens while other individuals had flowers with short styles and long stamens. This represents the first documented example of heterostyly in the Polemoniaceae. The morphological distinctions between these two entities and the heterostylous condition of the newly discovered populations support the recognition of the latter as a distinct species:

Gilia heterostyla S. Cochrane and A. Day, sp. nov. (Fig. 1)—Type: USA, Nevada, Nye Co., T3S R49E sect. 3, Gold Flat Rd 3.7 mi S of Cedar Pass Rd, Cactus Flat, 1705 m, 14 June 1978, *Susan A. Cochrane 1300* (holotype CAS; isotypes BRY, NY, RENO, RSA, UNLV, US).
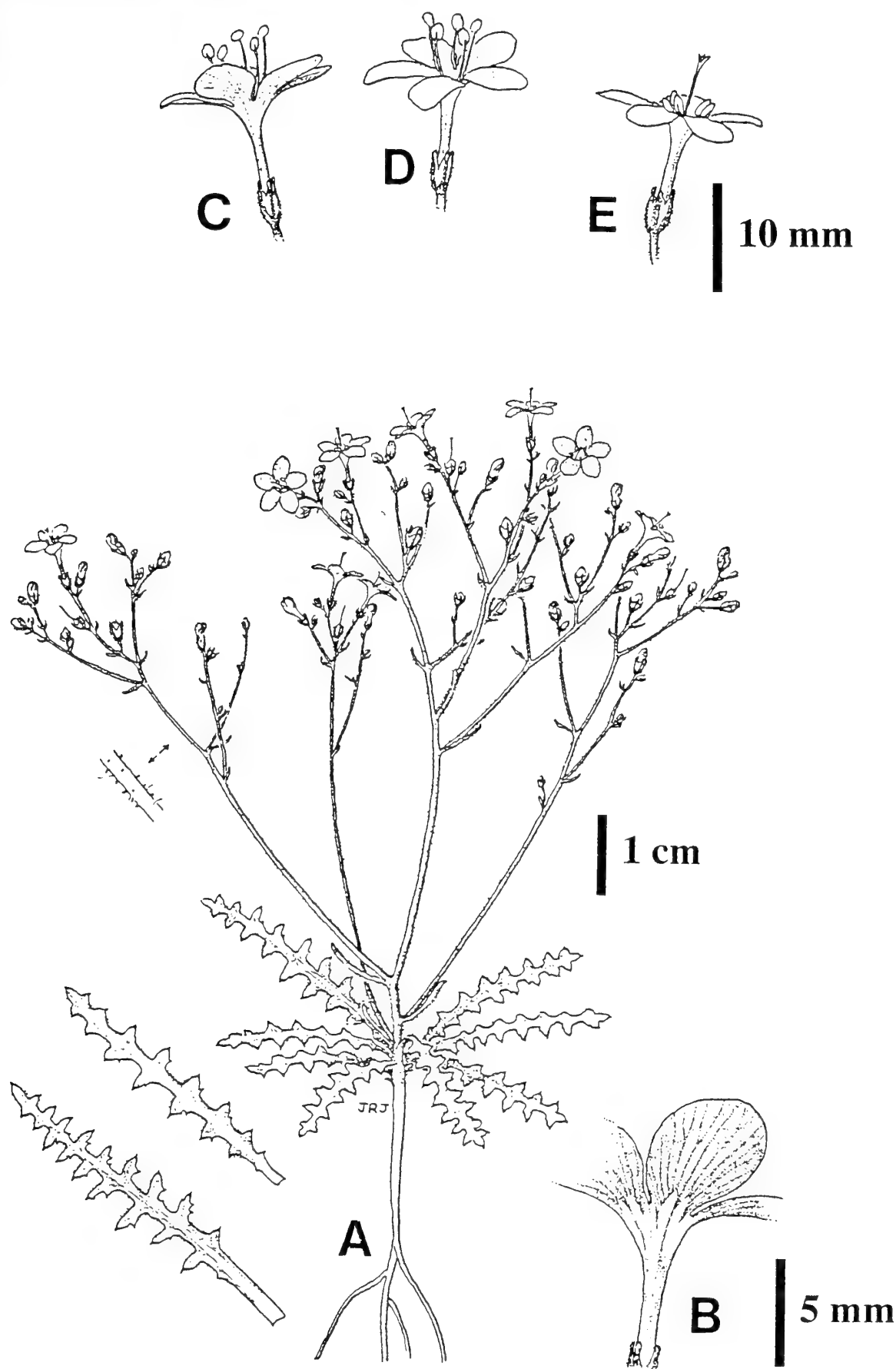
Fig. 1.   *Gilia heterostyla.* A. Habit. B. Abaxial surface of corolla showing veins. C and D. Pin flowers. E. Thrum flower.

Planta annua, erecta, glandulifer. Folia basalia et caulina, lineara-oblonga, pinnatifida bipinnatifidave, loba ad angulum 90 ad rhachis mucronata. Flores distyles. Corolla infundibuliforma, tubo 2–3 plo calycem, rosa-violacea vel alba liniis rosis-violaceis, faux dilatata anguste, longa quam lata, corolla macula bilobata flavo-virenti bilateraliter super venam roseo–violaceum instructa; lobi supri rosei vivide, infra rosei pallidi nervis atroviolaceis. Capsula calyce exserta. Semina 30–50 per capsulam. Chromosomatum numerum n = 8.

Erect annual 4–12 cm tall, branches 1–many from near base, moderately glandular puberulent throughout. Basal leaves in rosette, extended 1–3 cm up the stem, sometimes elevated on stem more than 1 cm above soil, glandular-puberulent and dotted with sand grains. Leaves linear-oblong, 0.5–7 cm long, 2–13 mm wide, rachis 0.4–2 mm wide, lower leaves pinnatifid to bipinnatifid, lobes at right angle to rachis, mucronate, 1–5 mm long, secondary lobes 0.5–2 mm long when present, usually on proximal margin of primary lobes. Lower cauline leaves 5–25 mm long, entire to pinnatifid; upper cauline leaves entire, gradually reduced to bracts 1–2 mm long at terminal branching points. Inflorescence corymbose-paniculate, in open to dense semi-hemispherical crown in many-branched individuals, pedicels 1–5 mm long. Flowers distylous. Calyx (pin and thrum) 2–3.5 mm long in flower, 3–4 mm in fruit, midrib green, sometimes purplish near tip or throughout, tip acuminate-apiculate, lobes $\frac{1}{3}$–$\frac{1}{2}$ length of calyx, hyaline membrane in the sinuses V-shaped, extended along margins to apex, growing with and usually not ruptured by capsule. Corolla (pin and thrum) funnelform, 11–17 mm long; tube narrow, 3–6 mm long, commonly 2(–3) times calyx, pink-violet or white with pink-violet streaks; throat narrowly flared, mostly as long as wide, 1–3 mm long, white with green-yellow bilobed spots centered on pink-violet midvein; lobes broadly ovate, subacute, 3–6.5 mm long, 4–6 mm wide, bright light pink above, paler below with darker veins. Stamens inserted near sinuses, filaments of pin flowers 1 mm long, anthers at orifice or to 1 mm above, filaments of thrum flowers 3–5 mm long, anthers exserted 3.2–5.5 mm above orifice; pollen cream colored. Ovary (pin and thrum) 2.5–3.3 mm long, green; styles of pin flowers 8–11 mm long, exserted 3.5–5 mm beyond corolla orifice; styles of thrum flowers 4–6(–9) mm long, not exserted beyond orifice. Stigmas white in both morphs, 1.1–1.2 mm long in pin flowers, 0.6–0.8 mm long in thrum flowers. Capsule (pin and thrum) 3.5–5 mm long, exserted beyond calyx, oblong ovoid, often purple-speckled at apex. Seeds 30–50, both pin and thrum plants setting abundant, normal-appearing seed. n = 8 in both morphs.

PARATYPES: USA: Nevada, Nye Co: In vicinity of "Five Mile," along Tonopah-Ely Hwy, 17 Jul 1937, *Goodner and Henning 766*

(RENO); 12 mi S of Hot Creek, 14 May 1941, *Eastwood and Howell 9448* (CAS); 10 mi NE of Warm Springs, 14 May 1941, *Eastwood and Howell 9454* (CAS, US); 7 mi S of Calloway, 26 May 1941, *Ripley and Barneby 3628* (CAS); 13 mi S of Hwy 25, N of playa, Kawich Valley Rd, 1 Jun 1968, *Reveal and Beatley 1116* (BRY, DS, NY, RENO, RSA, US, UTC); 14.2 mi NE of Warm Springs, Hwy 6, 28 May 1978, *Williams and Williams 78-74-5*; Alpha Gate (main entrance), Tonopah Test Range, Cactus Flat, 20 May 1978, *Williams 527* (CAS, NTS, UC); 2 mi N of Hwy 6, Saulsbury Wash Rd, S end Toquima Range, 27 May 1978, *Williams and Williams 78-62-1*; 5 mi NW of Gold Reed Pass, NE Gold Flat, 5250 ft, 3 Jun 1978, *Cochrane, Williams and Rhoads 1262* (CAS, NTS, RENO, RSA, US, UNLV); S of Monitor Hills, NW Cactus Flat, T1N R46E Sect 31 NW¼, 5 Jun 1978, *Cochrane, Williams and Rhoads 1281* (CAS, NTS); 0.4 mi E of Gold Flat Rd on Trailer Pass Rd, N Gold Flat, 5300 ft, 14 Jun 1978, *Cochrane 1302* (CAS, NTS, NY, RSA, UNLV); N boundary of Tonopah Test Range, W of main gate, N Cactus Flat, T1S R46E Sect 3, 15 Jun 1978, *Cochrane 1305* (CAS, NTS, UNLV, US, UTC); 14.2 mi NE of Warm Springs, Hwy 6, 26 June 1978, *Williams 78-142-3* (CAS); 0.4 mi E of Gold Flat Rd on Trailer Pass Rd, N Gold Flat, (chromosome count voucher), 15 May 1979, *Cochrane 1705* (CAS, NY, RENO, UNLV, US); Hwy 6, central Stone Cabin Valley, T3N, R48E, 20 May 1979, *Cochrane and Niles 1747* (CAS, NTS, RENO, UNLV); S end Hot Creek Valley, 20 May 1979, *Holland and Niles 2367* (CAS); 1 mi E of Five Mile Spring, Stone Cabin Valley, 20 May 1979, *Holland and Niles 2356* (CAS); Blue Jay Maintenance Station, Hwy 6, Hot Creek Valley, T6N, R51E, 28 May 1979, *Cochrane and Safford 1869* (CAS, NTS); along road, 1.0 mi W of Alpha Gate, N entrance to Tonopah Test Range, N Cactus Flat, T1S, R46E, Sect 1, 1 Jun 1979, *Cochrane 1895* (CAS, NTS); along power line rd, NE boundary of Tonopah Test Range, N Cactus Flat, T1S, R47E, Sect 4, 1 June 1979, *Cochrane 1899* (NTS); Ralston Valley S of Hwy 6, T1N, R45E, S27, 23 May 1981, *Williams and Tiehm 81-22-2* (CAS); E side Stone Cabin Valley, T4N, R49E, Sect 20, 23 May 1981, *Williams and Tiehm 81-21-1* (CAS); S of Locke's, Railroad Valley, 4.4 mi S of Hwy 6, T7N, R55E, Sect 4, 23 May 1981, *Williams and Tiehm 81-20-3* (CAS); between Currant and Nyala, 5.3 mi S of Currant, 11 Jun 1982, *Wilken 13849* (CAS); S end Pancake Range, E edge Big Sand Springs Valley, 2 rd mi N of Hwy 6 at the Black Rock lava flow, 5000 ft, T7N, R53E, Sect 9, 13 May 1987, *Knight 1564* (NY).

Distribution. Gilia heterostyla occurs in deep alluvial sands on floors and lower slopes of north–south trending Basin and Range valleys of northern Nye County, Nevada, at an elevational range of 1463–1828 m. It is known from Cactus Flat, southeast of Tonopah,
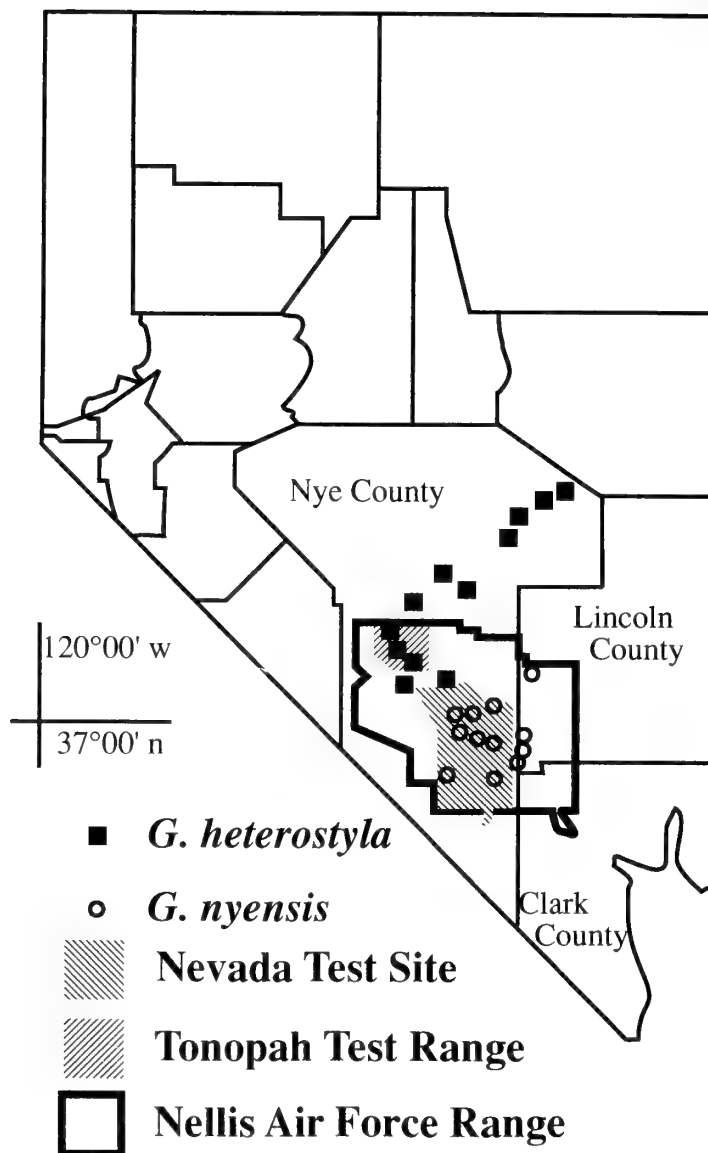
FIG. 2. Distribution of *Gilia heterostyla* and *Gilia nyensis* in south central Nevada.

east and north to the dunes in eastern Railroad Valley (Fig. 2). Recent treatments have considered these populations as *G. nyensis* (Cronquist, 1984).

Habitat and phenology. Gilia heterostyla flowers from May to early July. It grows in open areas and under shrubs in Great Basin vegetation typical of sandy valley floor habitats dominated by *Atriplex canescens* and *Achnatherum hymenoides.* Other commonly associated shrubs include *Chrysothamnus greenei, Tetradymia glabrata* and *Psorothamnus polydenius.*

Morphology. Pin and thrum flowers do not differ morphologically except in stamen, style, and stigma lengths. Stigmatic papillae appear the same in both morphs. Estimates of pollen fertility appear equally high (89–99%) in pin and thrum flowers of *G. heterostyla,* as determined from staining grains with lactophenol-cotton blue. Measure-

TABLE 1. COMPARISON OF MORPHOLOGICAL FEATURES OF *GILIA HETEROSTYLA* AND *G. NYENSIS*.

Character	G. heterostyla	G. nyensis
Floral morphology	Distylous	Homostylous
Leaf lobe posture	Right angle to rachis	Ascending tipward
Leaf lobe width	Broad at rachis	Narrow at rachis
Corolla lobe color		
Upper surface	Bright light pink	Dark magenta
Lower surface	Bright light pink	Pale milky pink
Corolla lobe veins	Purple	Not apparent
Corolla tube	Well-exserted	Included in calyx
Corolla throat	Gradually expanded	Abruptly expanded
Capsule	Exserted from calyx	Generally included
Seeds/capsule	30–50	Generally 14–30

ments of pollen grain diameters in the two morphs also showed no significant differences. Pollen is zonocolporate with striato-reticulate sexine in pin and thrum flowers.

One population of *G. heterostyla* sampled in the field showed nearly equal numbers of pin and thrum plants. Herbarium collections with large numbers of plants on single sheets also had nearly identical numbers of pin and thrum plants.

Chromosome counts of $n = 8$ for *G. heterostyla* were made from pollen mother cells of pin and thrum plants (voucher *Cochrane 1705*). We also counted $n = 8$ for *Gilia nyensis* (voucher *Cochrane 1904* CAS). This differs from a report of $n = 9$ for *G. nyensis* by Reveal & Styer (1973). We have seen a duplicate of their cited voucher and verified that it is *G. nyensis*. Diploid chromosome numbers of both $n = 8$ and $n = 9$ are known in section *Giliandra* (Grant 1959), as in the related *G. hutchinsifolia* Rydb. with $n = 9$ (Grant l. c.) and *G. subacaulis* Rydb. with $n = 8$ (Day 1993). Further studies of chromosome number and relationships in sect. *Giliandra* are to be reported elsewhere by the second author.

Relationship with G. nyensis. Gilia heterostyla differs from *G. nyensis* most significantly by its distylous flowers; however, there is an array of floral and vegetative characters that distinguish these species of section *Giliandra* (Table 1).

Corolla color differs noticeably between the two species in fresh material. Corollas of *G. heterostyla* are bright light pink, whereas those of *G. nyensis* are dark magenta, almost hot pink. In herbarium specimens the corollas of both species dry to blue, but those of *G. nyensis* become darker blue than those of *G. heterostyla*. The outer (abaxial) surface of the lobes of *G. heterostyla* is the same color as the inner (adaxial) surface, with darker veins prominent, while the abaxial surface of *G. nyensis* lobes is paler milky pink than the adaxial surface, and veins are not apparent. The corolla tube of *G.*

heterostyla is the same color as the lobes; in *G. nyensis* the tube is violet. Both species have green-yellow spots in the throat below each corolla lobe, as do *G. hutchinsifolia* and *G. subacaulis* also of section *Giliandra*. In *G. heterostyla* the spots appear paired, as they are bisected by a purple midvein, while the spots in *G. nyensis* appear singly, and are not bisected by a colored midvein. Furthermore, the stigmas of *G. heterostyla* are always white, while those of *G. nyensis* are often streaked with purple.

These two species also differ in corolla size and shape. The corolla tube of *G. heterostyla* is over twice the length of the calyx, while that of *G. nyensis* is slightly if ever exserted beyond the calyx. The throat of *G. heterostyla* is more gradually and narrowly flared than that of *G. nyensis,* which flares abruptly at almost a 45 degree angle, and is often wider than long.

The pinnatifid leaf segments of *G. heterostyla* extend perpendicular to the rachis, as seen in *G. subacaulis,* while in *G. nyensis* the segments angle forward, a characteristic shared with *G. hutchinsifolia* and *G. pinnatifida.* Nutt.

These species are also distinguished by ecological preferences. *Gilia heterostyla* occurs in open sandy flats in large valleys, while *G. nyensis,* found mostly to the south of *G. heterostyla* (Fig. 2), is restricted to deep sands derived from volcanic tuff on mountains, mesas and in valleys. It grows in the Great Basin–Mojave Desert transition zone, in *Artemisia*-Piñon-Juniper, *Grayia-Tetradymia-Artemisia tridentata-Atriplex confertifolia-Psorothamnus polydenius, Coleogyne* and *Larrea-Ambrosia* vegetation. These two species have not been found growing sympatrically, although potential areas of sympatry may exist on restricted-access military lands. Populations of these species have been found at opposite ends of Kawich Valley. No morphological intergradation between these species has been noted.

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NOTE

EXTRAFLORAL NECTARIES ON *ARBUTUS MENZIESII* (MADRONE). — John C. Hunter, Section of Plant Biology, University of California, Davis, CA 95616.

From April to July 1993, I made observations on the vegetative buds of *Arbutus menziesii* (Ericaceae) growing at the University of California's Northern California Coast Range Preserve in Mendocino County. During bud burst and the early stages of leaf expansion, these buds appeared to function as extrafloral nectaries. This has not been previously documented for *Arbutus.*

On branches where the apical bud had begun to swell and burst, a droplet of fluid exuded from the tip of the apical and the upper axillary buds. This fluid tasted faintly sweet, and tested positive for reducing sugars (using Benedict's solution). I observed various Coleoptera, Diptera, and Hymenoptera on the buds, the most abundant of which was the ant *Prenolepis imparis* Say.

Inside the buds, the nectar was exuded from the adaxial surface of the bud scales. On this surface, free-hand sections revealed glandular trichomes that may be the source of the nectar. These trichomes were typically 250–600 nm long and consisted of up to two dozen cells arranged into a basal stalk and a wider head. The trichomes, and frequently adjacent epidermal cells, were densely stained with neutral red, as is commonly seen in active nectaries (Kearns and Inouye, Techniques for Pollination Biology, 1993).

On four trees, I monitored 18 apical and 117 axillary buds on 18 marked branches. During the period of bud burst (April–May), all apical buds and 63 of 117 axillary buds exuded nectar. During leaf expansion, the bud scales reflexed, withered, and abscised. Only 3 of the 63 axillary buds that produced nectar gave rise to fully developed shoots; the others abscised during the summer along with the previous year's leaves and bark.

Extrafloral nectaries are often most active during the period of leaf expansion (Darwin, Journal Linnean Society of London 15:398–409, 1876; Tilman, Ecology 59: 686–692, 1978; Curtis and Lersten, American Journal of Botany 61:835–45, 1974). They are suggested to reduce herbivory by attracting ants that deter herbivores (Bentley, Annual Review of Ecology and Systematics 8:407–427, 1977), and experimental evidence supports this interpretation (Oliviera et al., Oecologia 74:228–230, 1987; Koptur, Ecology 65:1787–1793, 1984). The extrafloral nectaries of *Arbutus menziesii* also may serve this function.

SEED PRODUCTION AND SEED PREDATION IN
GENTIANA NEWBERRYI (GENTIANACEAE)
POPULATIONS

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ABSTRACT

In the Sierra Nevada, flowers of *Gentiana newberryi* Gray were significantly larger and produced more ovules at Little Valley (2000 m) and Forestdale Divide (2580 m) than at Frog Lakes (3120 m). The mean number of seeds produced at Little Valley was significantly larger. Predation reduced seed set at the higher elevation sites. Herbivores removed 37.9% of the flowers at Frog Lakes. Predispersal seed predators (Diptera larvae) consumed all of the seeds in 64.3% of the capsules at Forestdale Divide and 3.0% at Frog Lakes. Later blooming flowers experienced less predation but risked permanent snow cover before the seeds matured.

Successful reproduction in plants is influenced by availability of resources (Stephenson 1981; Evenson 1983; McDade and Davidar 1984; Harder et al. 1985; Stanton et al. 1986; Primack 1987; Horvitz and Schemske 1988; Primack and Kang 1989) and pollinators (Levin and Anderson 1970; Bierzychudek 1981; Thomson 1981; Pleasants 1983; Waser 1983; Motten 1986; Galen and Newport 1988; Ashman and Stanton 1991) and the ability to avoid predation (Louda 1982a, b, 1983; Crawley 1988). Factors affecting seed set may vary from year to year and among populations (Douglas 1981; Campbell 1987). In areas where resources and pollinators are unpredictable, a successful perennial plant should be able to set seeds or produce seedlings under a variety of limitations (Sutherland 1986). While self-fertilized (Levin 1971; Jain 1976; Barrett 1988; Karoly 1992) and vegetatively produced plants (Evenson 1983; Waller 1988) increase the number of genetically identical plants in the population and can increase the risk of inbreeding depression, those plants that are successful may have coadapted genes that are advantageous for the current environmental stresses experienced by the population (Lloyd 1979; Waser and Price 1983; Barrett 1988).

Flower removal by herbivores and predispersal seed predators can limit the number of seeds produced by a population (Janzen 1971; Arnold 1982; Louda 1982a, b; 1983; Crawley 1988; Hendrix 1988). The rates of herbivory and seed predation in a species have been found to vary between sites and along a climatic gradient (Louda 1982a, 1983).

Gentiana newberryi Gray is restricted to high elevation wet meadows in eastern California, western Nevada, and southern Oregon (Hickman 1993). A perennial, *G. newberryi* has protandrous funnel shaped flowers with corollas that are usually white with greenish spots (Munz 1973). In the White Mountains, California (3550 m elevation), *Gentiana newberryi* is visited by *Bombus sylvicola* Kirby, *Bombus balteatus* Dahlbom, *Bombus huntii* Greene, and *Bombus morrisoni* Cresson (Spira 1983; Spira and Pollak 1986). Flowers under insect exclosures in the White Mountains did not produce mature fruits or seeds (Spira 1983; Spira and Pollak 1986) but *G. newberryi* in Little Valley, Nevada did produce viable seeds (Barnes and Rust 1994). When flowers under exclosures in Little Valley were supplemented with pollen from a flower on the same plant, there was no difference in the number of seeds produced when compared with cross-pollinated flowers (Barnes and Rust 1994). Spira (1983) found 2.9–3.6 vegetative rosettes per plant in the White Mountains. In Little Valley 90% of ramets observed had at least one lateral rhizome. Spira (1983) and Spira and Pollak (1986) observed marmots and noctuid moth larvae consuming *G. newberryi* flowers but not fruits or seeds. Predispersal capsule predation of *Gentiana saponaria* L. by *Endothenia habesana* Walker (Lepidoptera) larvae has been observed to reduce seed set by 94% (Windus 1990).

We investigated the differences in seed set per flower in three populations of *Gentiana newberryi* at different elevations in the Sierra Nevada. We measured soil water potential and recorded pollinator visits to determine if limitations influencing seed set were similar at each site. Flowers were examined for evidence of herbivory or capsule predation.

Methods and Materials

Study sites. In July 1992, three study sites were established in flat montane meadows before flowering and were followed weekly until snowfall covered the areas. These sites were located along the eastern edge of the Sierra Nevada escarpment at elevations from 2000 to 3120 m. The Little Valley site (119°52′W, 39°15′N) in Washoe Co., Nevada is located in the Whittell Forest and Wildlife Area owned by the University of Nevada, Reno (elev. 2000 m). The Forestdale Divide site (119°58′W, 38°40′N) in Alpine Co., California is located in the Toiyabe National Forest (2580 m). The Frog Lakes site (119°17′W, 38°3′N) is in the Hoover Wilderness area of the Toiyabe National Forest in Mono Co., California (3120 m). All three meadow sites are covered by snow during the winter and collect and retain water from snow melt longer than surrounding areas. This study was conducted during the sixth year of a drought (James 1992). Snowfall was about 50% of normal and melted earlier than usual from all three sites (James 1992).

Seed production. Each week, at each site, 10–20 *G. newberryi* flowers that had newly opened corollas and dehiscing anthers were marked and numbered. Flower phenology was observed and each marked flower was checked weekly for signs of herbivore damage. When capsules matured (usually 3–4 weeks after flower opening), the flowers were removed and stored in individual waxed paper bags. The number of mature seeds and undeveloped ovules in each capsule was counted. The female reproductive potential for *G. newberryi* flowers at each site was estimated by calculating the mean number of mature seeds produced by the marked flowers. The total number of ovules produced and the percentage of ovules that produced mature seeds were also determined. After counting, the mature seeds from each flower were placed in individual waxed paper bags and stored outdoors. Capsules with Diptera larvae were placed in individual clear plastic vials with air holes for overwintering and rearing.

Mature seeds from three to four randomly chosen flowers at each site were used to estimate germination potential. Thirty to fifty seeds from each flower were placed in a separate petri dish on brown paper over kimpack moistened with a 400 ppm gibberellic acid solution. The seeds were kept at 15°C for 7 days and then alternated between 15°C for 12 hr and 25°C for 12 hr for 14 days. The percentage of seeds germinated at each site was calculated.

Flower predation. All collected *G. newberryi* capsules were checked for evidence of capsule predators. Capsules that contained insect-damaged seeds were examined to determine if any intact mature seeds remained.

Marked flowers were examined for any evidence of herbivore damage. If flower tags were missing or no longer attached to a flower then the flower was assumed to have been removed by an herbivore. The sites were monitored weekly for the presence of herbivores that could potentially consume *G. newberryi.*

Floral characteristics and pollinators. Corolla length and maximum corolla tube width of *G. newberryi* flowers were measured during the second week in August in several areas of each site. A flower size index was developed by multiplying corolla length by corolla tube width. Nectar volume was measured at each site using capillary tubes. The soil moisture potential was measured with a Quickdraw Series 2900 Soil Moisture Probe where the flowers were measured.

Bees or other potential pollinators were rarely observed at the Forestdale Divide or Frog Lakes sites, so all visits were recorded. At Little Valley, hourly transects were walked twice each week and all flower visits by bees were recorded (Barnes and Rust 1994). Beginning in September, when bees were rare at Little Valley, all

TABLE 1.   COMPARISON OF *GENTIANA NEWBERRYI* FLOWER SIZE AT THREE SITES IN THE SIERRA NEVADA DURING THE SECOND WEEK OF AUGUST 1992. Values are means ± standard deviation. [1] Index developed by multiplying corolla length by maximum corolla width to compare sites. [2] Bonferroni t-tests, means with the same letter are not significantly different (P < 0.05).

Site	Corolla length (mm)	Corolla width (mm)	Flower size index[1]	n	Bon-Grp[2]
Little Valley	40.7 ± 5.6	12.7 ± 3.1	530.4 ± 188.2	50	A
Forestdale Divide	38.3 ± 3.7	13.0 ± 2.0	495.1 ± 68.5	16	A
Frog Lakes	25.8 ± 4.1	7.0 ± 2.2	187.2 ± 90.3	25	B

observed insect visits to flowers were recorded. Samples of all insect visitors at each site were collected for identification by R. Rust, University of Nevada, Reno and R. Brooks, University of Kansas, Lawrence.

Statistical analyses. Analysis of variance (GLM in SAS 1990) was used for all comparative analyses within and between populations. Arcsine transformations were used for analysis of percentage data and other cases which violated assumptions. When analysis of variance indicated a significant difference, a Bonferroni t-test was used for pairwise comparisons within and between populations. Linear regression (SAS 1990) was used to determine if there was a relationship between soil moisture and flower size at each site.

RESULTS

Floral characteristics and pollinators. Flowering of *G. newberryi* began during the first week in July at Little Valley and the first week in August in Forestdale Divide and Frog Lakes and continued until the second week in October at all three sites. *Gentiana newberryi* corollas at Little Valley and Forestdale Divide were similar in size but the corollas at Frog Lakes were significantly smaller (F = 45.01, df = 2,88, P < 0.0001) (Table 1). Linear regression showed a significant relationship between soil moisture and corolla size in Little Valley (F = 117.78, df = 1,48, P < 0.0001) with the larger flowers found in wetter soil (Table 2). The regression of flower size and soil moisture was not significant at Forestdale Divide (F = 1.02, df = 1,14, P = 0.3309) or Frog Lakes (F = 2.22, df = 1,23, P = 0.1500) (Table 2).

Nectar was available in most *G. newberryi* flowers at each site throughout the study. The mean amounts of nectar available (mm/1 lambda capillary tube) per flower at Little Valley (23.0 ± 13.2 (SD)), Forestdale Divide (25.4 ± 16.1), and Frog Lakes (6.6 ± 3.7) were not significantly different (F = 0.06, df = 2,12, P = 0.0627).

TABLE 2. WITHIN SITE COMPARISONS OF SOIL WATER POTENTIAL AND *GENTIANA NEWBERRYI* FLOWER SIZE AT THREE STUDY SITES IN THE SIERRA NEVADA DURING THE SECOND WEEK OF AUGUST 1992. Flower size index values are means ± standard deviation. [1] Index developed by multiplying corolla length by maximum corolla width. [2] Bonferroni t-tests comparing flower size within each site. Means with the same letter are not significantly different (p < 0.05).

Site	Soil water potential (KPa)	Flower size index[1]	n	Within site BonGrp[2]
Little Valley	0	764.1 ± 79.0	10	A
	4	617.6 ± 106.8	10	B
	8	557.7 ± 106.0	10	B
	18	425.1 ± 102.3	10	C
	35	287.5 ± 74.4	10	D
Forestdale Divide	0	508.6 ± 72.6	6	A
	9	512.8 ± 23.0	5	A
	15	460.4 ± 97.3	5	A
Frog Lakes	0	140.6 ± 33.9	5	A
	6	141.2 ± 27.8	5	A
	10	221.5 ± 120.2	10	A
	19	210.8 ± 74.1	5	A

Bombus vosnesenskii Radoszkowski, *B. edwardsii* Cresson, *Anthophora bomboides* Kirby, *A. urbana* Cresson, *A. terminalis* Cresson, and *Apis mellifera* L. were the most common visitors to *G. newberryi* in Little Valley. The frequency of bee visits decreased rapidly from the onset of flowering in early July. Only one bee was seen after August even though there were *G. newberryi* flowers with nectar and pollen available until early October. In September, one *B. edwardsii* was observed visiting *G. newberryi* at Forestdale Divide. Small syrphid flies, *Eupeodes volucris* Osten Sacken, were the only other visitors observed at this site. A total of ten visits by *B. vosnesenskii* and *B. edwardsii* were observed over two months at Frog Lakes. Bumble bees were rare in the Sierra Nevada in 1992, compared to most years (R. Rust and R. Thorp personal communication). *Bombus edwardsii, B. vosnesenskii,* and *Bombus appositus* Cresson were observed throughout the day in Little Valley in 1991 from August 1 through September 27 (Barnes and Rust 1994) but few were seen in 1992. *Gentiana newberryi* flowers close at night and open the following morning. Therefore, flowers were not monitored for nocturnal pollinator activity.

Seed production. The mean number of ovules per flower at Little Valley (232.0 ± 94.7, n = 82) and Forestdale Divide (186.7 ± 68.6, n = 12) was significantly higher than at Frog Lakes (118.2 ± 72.5, n = 10) (F = 7.76, df = 2,101, P = 0.0007). The mean number of

mature seeds produced per capsule in all marked flowers was significantly higher in Little Valley (131.6 ± 112.9, n = 84) than at Forestdale Divide (10.3 ± 33.3, n = 97) or Frog Lakes (13.8 ± 44.2, n = 68) (F = 76.02, df = 2,246, P < 0.0001). There was no significant difference in the percent of seeds that germinated at Little Valley (84.8% ± 11.1%), Forestdale Divide (46.8% ± 33.1%) or Frog Lakes (59.4% ± 31.5%) (F = 2.11, df = 2,8, P = 0.1840).

Floral predation. Predation by mammalian flower herbivores and/ or insect predators of capsules was found at Forestdale Divide and Frog Lakes but not at Little Valley. When marked flowers that were damaged or removed by predators are excluded from the analysis, the mean number of mature seeds produced per capsule is significantly higher at Little Valley (131.6 ± 112.9, n = 84) than at Forestdale Divide (41.5 ± 57.2, n = 24) or Frog Lakes (39.1 ± 68.2) (F = 13.24, df = 2,129, P < 0.0001).

Capsules containing Diptera larvae or with all seeds damaged occurred in 64.3% of all capsules at Forestdale Divide and in 3.0% at Frog Lakes. All seeds within the capsule were eaten before pupation. The number of seeds produced per capsule in marked flowers was significantly reduced by Diptera larvae at Forestdale Divide (F = 12.29, df = 1,119, P = 0.0006) but not at Frog Lakes (F = 0.03, df = 1,48, P = 0.8749).

No mammalian herbivore damage to *G. newberryi* plants or flowers was observed at Forestdale Divide. At Frog Lakes 37.9% of marked flowers were removed by mammalian herbivores. The reduction in the number of mature seeds produced per marked flower was not significant (F = 3.35, df = 1,90, P = 0.0704). During week four (September 5), only five intact flowers were found on the study site and many corolla tubes were found on the ground. No herbivores were ever observed foraging on *G. newberryi,* but many flowers on the ground had the base of the corolla tube missing. During week five (September 12), many more flowers were present and of 20 marked only one was removed by herbivores. These marked flowers produced significantly more seeds per capsule than flowers marked in previous weeks (F = 4.82, df = 2,63, P = 0.0112).

Common potential herbivores observed in the area were yellow bellied marmots (*Marmota flaviventris*), pikas (*Ochotona princeps*), Belding's ground squirrel (*Citellus beldingi*), and alpine chipmunks (*Eutamius alpinus*).

DISCUSSION

The flower size and number of ovules produced per *G. newberryi* flower were not significantly different between Little Valley (2000 m) and Forestdale Divide (2580 m). The flowers at Frog Lakes (3120 m) were smaller and had fewer ovules. This suggests that ovule

number may be related to flower size. High elevation plants and flower size are frequently limited by cold temperatures and desiccating winds (Billings and Mooney 1968, Bliss 1971, Douglas 1981) and a shorter snow free growing season. They are often smaller than the same species at lower elevations. Size variation in *G. newberryi* is correlated with altitude and moisture (Hickman 1993). Little Valley had more variation in flower size and soil water potential suggesting that soil water was an important limiting resource at this site but not at the higher elevation sites.

There is no significant difference in the percentage of ovules that produce mature seeds at the three sites if only seed capsules with some mature seeds are considered. This excludes aborted seed capsules and herbivore damaged capsules. Predation by flower herbivores at Frog Lakes and Diptera larvae at Forestdale Divide are responsible for the large difference in the number of mature seeds produced. Nearly 65% of the seed capsules at Forestdale Divide and 3% at Frog Lakes had all seeds damaged. More capsules aborted or were unable to mature seeds due to early snowfall at the higher elevation sites than at Little Valley.

A significant reduction in seed set due to insect damage to seeds has been observed in other species of *Gentiana* (Windus 1990). However, no seed capsule predators were reported on *G. newberryi* in the White Mountains, California (3550 m) (Spira 1983, Spira and Pollak 1986). It is not apparent why the Diptera larvae are frequently found at two higher elevation sites at Forestdale Divide (2580 m) and Frog Lakes (3120 m) and not at Little Valley (2000 m) or the White Mountains. Louda (1982a) found predispersal seed predator numbers decreased over a climatic gradient from the coast to the mountains in *Haplopappus squarrosus* Hook. & Arn. and that high predator numbers contributed to lower recruitment and plant densities at lower elevations. The Forestdale Divide population is small and the high seed predation losses may be an important factor in limiting population size.

Yellow bellied marmots, pikas, Belding's ground squirrels, and alpine chipmunks were common around Frog Lakes until mid-September. Many marked *G. newberryi* flowers were removed by herbivores during August and corolla tubes were found on the ground with the base of the flower missing. During week four (September 5), there were only five *G. newberryi* flowers found at the site and many corolla tubes were found on the ground. It seems that flowers were removed as soon as they opened. The 38% of marked flowers removed by herbivores probably underestimates the impact of herbivores on seed production since flowers were removed before being marked for study. The following week (September 12), over 60 newly opened flowers were found but no marmots, grounds squirrels or chipmunks were detected. Of the flowers marked that week, only

one was removed. Marmots appeared to be the primary herbivores on *G. newberryi* flowers in the White Mountains, California (Spira 1983, Spira and Pollak 1986). Plants that flower after many of the herbivores begin hibernating reduce herbivore risk but are exposed to nightly freezing temperatures, occasional snowfall, fewer pollinators and risk snow cover before seeds have time to mature.

As a facultative self-compatible perennial, *G. newberryi* has numerous adaptations that allow populations to persist with different and unpredictable abiotic and biotic limitations. The late flowering period may reduce predation and competition for pollinators (Zimmerman 1980, Thomson 1981, Gross and Werner 1983) and when pollination is insufficient, self-pollination can produce viable self-fertilized seeds (Sutherland 1986, Barrett 1988, Barnes and Rust 1994). Vegetative reproduction requires less energy (Waller 1988) and new ramets can be produced when predators are removing flowers and seeds. The variance in predator pressure, pollinator availability, and ovule number result in different reproductive limitations among the sites. Resource differences can result in differences in flower size within and among populations. The amount and time of snowfall and other climatic factors vary among sites at different elevations and among years. Since factors influencing the reproductive output of a perennial species can be highly variable, it is important to document the variation within and among populations when trying to identify the adaptive value of observed life history traits.

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POLLINATION BIOLOGY OF *STREPTANTHUS TORTUOSUS* (BRASSICACEAE)

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Abstract

I measured floral characters, recorded floral visitors, and observed pollinator behavior in populations of *Streptanthus tortuosus* over an elevation gradient (305–2967 m). Floral characters differ significantly among populations with a negative correlation between flower size and elevation. Flowers from both high and low elevation populations are self-compatible but set few seeds in the absence of pollinators. Bees are the most common and consistent floral visitors, although wasps, flies, butterflies, and beetles were also observed visiting the flowers. Floral differences do not appear to be linked to breeding system differences or to pollinator differences but may instead be associated with some other phenomenon, such as climatic adaptation.

Floral variation in the genus *Streptanthus* has been well documented (Greene 1904; Hoffman 1952; Kruckeberg 1957; Kruckeberg, Rodman and Worthington 1982; Dolan and LaPre 1989). Flower size, shape, orientation, and color vary both among and within species. Although floral variation among species may be due to differing pollination biology (Rollins 1963; Rollins and Holmgren 1980), little is known about the pollinators or breeding systems of *Streptanthus* species (Al-Shehbaz 1985). Kruckeberg (1957) noted that *S. glandulosus* was self-compatible and that self-pollination was prevented by a combination of protandry and herkogamy. Rollins (1963) reported that *S. cutleri* and *S. carinatus* were strongly protandrous and self-incompatible and that nectar production coincided with the beginning of the pistillate phase.

Kruckeberg (1957) observed that bees appeared to be the most abundant visitors, although flowers were also visited by butterflies, beetles, and even hummingbirds. Moldenke (1976) reported that butterflies and syrphid flies were the major pollinators of *Streptanthus* species in the Sierra Nevada of California. He also listed *Bombus, Andrena,* and *Osmia* as genera of "important bee pollinators" of *Streptanthus.*

In this study, I examined the pollination biology of *Streptanthus tortuosus* Kellogg, a species that is widespread on rock outcrops and dry rocky slopes in the Sierra Nevada and in the Coast Ranges of northern California and southern Oregon. Although flowers in all populations are strongly protandrous and herkogamous (Preston

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1991), populations show wide variation in floral and vegetative traits. The object of this study was to determine if floral variation in *S. tortuosus* populations is associated with differences in breeding systems, pollinators, or pollinator behavior.

The principal hypothesis tested was that smaller flower size is an indication of increased self-pollination. Fewer pollinators and lower floral visitation rates at high elevations may explain the increasing proportion of autogamous species associated with increasing elevation (Mani 1962; Moldenke 1979; Arroyo et al. 1985). Smaller flowers and lower pollen–ovule ratios are expected to evolve under increased selfing (Solbrig 1976; Lloyd 1979; Charlesworth and Charlesworth 1981; Charnov 1982), and indeed, floral parts of autogamous species are typically much smaller than those of related allogamous species (Lloyd 1965; Ornduff 1969; Wyatt 1983). Additionally, the proportion of resources allocated to male function is relatively lower (Cruden 1977; Cruden and Lyon 1985; McKone 1987; Schoen 1982). The second hypothesis tested was that pollinators differ among populations in a pattern correlated with floral variation.

MATERIALS AND METHODS

Sites. Observations and sampling were done at six sites over a broad portion of the range of *S. tortuosus*. Three sites were selected at lower elevations and three at higher elevations: Table Mountain (Butte County, 39°36'N, 121°33'W, elevation 400 m), Coulterville (Mariposa County, 37°38'N, 120°09'W, elevation 548 m), Oregon Mountain (Trinity County, 40°44'30"N, 123°00'W, elevation 762 m), Mount Shasta (Siskiyou County, 41°21'30"N, 122°12'W, elevation 2316 m), Carson Pass (Alpine County, 38°42'N, 119°59'W, elevation 2360 m), Tioga Pass (Mono County, 37°55'30"N, 119°15'30"W, elevation 2967 m). Voucher specimens from all populations were deposited in the John M. Tucker Herbarium, University of California, Davis.

Floral Morphology. At each of the sites I measured sepal and petal lengths of one flower each from 20–60 plants. All measurements were made on fully opened flowers that had not yet begun to senesce. Flowers were collected from approximately the same level on the main raceme because flowers appear to be smaller towards the raceme tips and on lateral racemes. I also collected one flower bud each from 20–30 plants and preserved them in 80% ethanol for pollen analysis.

I counted the number of ovules in each flower bud. I determined pollen grain number and diameter in one upper, lower, and lateral anther by dissecting the anthers into a 2% saline solution to disperse

the pollen grains, counting them with an electronic particle analysis system (Karuhn and Berg 1984; Stanton and Preston 1988). I calculated the pollen–ovule ratio for each bud by multiplying the number of pollen grains by two and then dividing by the number of ovules. I estimated pollen viability by dissecting the other three anthers from each bud into a pollen mounting medium containing aniline blue and determining the proportion of stained (viable) vs. unstained (non-viable) pollen grains.

Breeding system. To measure self-compatibility and autofertility, I raised plants from seeds collected from two representative populations, Table Mountain and Carson Pass. I grew seedlings in a greenhouse on the campus of U.C. Davis, and placed them outside from mid-December to mid-March to induce flowering. Greenhouse-grown plants from Carson Pass did not flower normally under these conditions; therefore I transplanted plants with flower buds from Carson Pass to the greenhouse at Davis. On each plant, I cross-pollinated or self-pollinated several randomly chosen flowers, leaving the remainder unpollinated. Each cross-pollinated flower received pollen from a single donor flower, chosen randomly from among the other greenhouse progeny. Self-pollinations were done geitonogamously using pollen from an adjacent recently opened flower. Pollen was transferred from freshly opened anthers to fully expanded stigmas with a flat toothpick, which was cleaned between pollinations. To determine fruit and seed set, I collected fruits when the seeds were fully mature.

Pollinator observations. From 1984 to 1988, I made observations and collections of floral visitors on warm, clear, windless days, during peak flowering at the six study sites. I identified floral visitors by comparison with specimens in the Bohart Museum of Entomology at the University of California, Davis. All insect voucher specimens were deposited at the Bohart Museum.

RESULTS

Floral characters. Floral characters differed significantly among populations (Table 1) and showed a clear pattern to the variation. Plants from populations at higher elevations had significantly shorter petals and sepals and produced significantly fewer pollen grains and fewer ovules per flower. Moreover, pollen–ovule ratios were lower in populations at higher elevations. Pollen viability appeared to be uniformly high, averaging 97.6% (SE = 0.63) across all populations.

Breeding system. Fruit-set did not differ significantly between cross-pollinated and self-pollinated flowers in Table Mountain plants (χ^2 = 0.048, P > 0.78) or in Carson Pass plants (χ^2 = 0.116, P > 0.74), nor did fruit-set differ between the two populations (χ^2 = 0.018, P

TABLE 1. POPULATION MEANS OF FLORAL CHARACTERS MEASURED FOR 6 POPULATIONS OF *STREPTANTHUS TORTUOSUS*. Standard deviations and sample sizes are given in parentheses. Means in each column identified by the same letter are not significantly different.

Population	Elevation (m)	Petal length (mm)	Sepal length (mm)	Pollen grains/flower	Ovules/flower	Pollen/ovule	Pollen grain diameter (μm)
Table Mountain	305	12.5[a] (1.01; 61)	10.1[a] (0.97; 61)	449,533[a] (62,269; 20)	67.8[a] (9.05; 24)	6754[a] (1248; 20)	14.80[a] (0.675; 24)
Coulterville	548	13.6[b] (1.00; 60)	11.1[b] (1.01; 60)	582,224[b] (52,004; 20)	58.4[b] (11.54; 27)	10,063[b] (2191; 20)	14.62[a,b] (0.601; 27)
Oregon Mountain	762	14.6[c] (1.16; 40)	11.3[b] (1.07; 40)	369,499[a] (120,561; 25)	62.6[a,b] (11.22; 31)	5943[a,c] (1715; 25)	14.71[a,b] (1466; 24)
Mount Shasta	2316	9.4[d] (0.68; 20)	7.0[c] (0.66; 20)	209,234[c] (26,500; 20)	41.5[c] (6.36; 24)	5054[c] (635; 20)	14.47[a,b] (0.850; 24)
Carson Pass	2630	9.6[d] (0.76; 30)	7.6[c] (0.65; 30)	193,847[c] (59,747; 20)	34.8[c] (5.22; 24)	5560[a,c] (1487; 20)	13.95[b] (0.746; 19)
Tioga Pass	2967	9.1[d] (0.75; 30)	7.2[c] (0.68; 30)	125,511[c] (42,515; 20)	40.3[c] (8.77; 30)	3035[c] (700; 20)	14.10[a,b] (0.710; 20)

TABLE 2. MEAN PROPORTION OF POLLINATED FLOWERS PRODUCING MATURE FRUITS AND MEAN PROPORTION OF OVULES PRODUCING MATURE SEEDS FOR EXPERIMENTALLY CROSS- AND SELF-POLLINATED FLOWERS IN PLANTS FROM TWO POPULATIONS OF *STREPTANTHUS TORTUOSUS*. Means in each column identified by the same letter are not significantly different.

Population	Treatment	Number	% Fruit-set (flowers)	% Seed-set (fruit)
Table Mountain	Cross-pollinated	106	74.0 (457)[a]	50.8 (330)[a]
	Self-pollinated	102	75.9 (469)[a]	43.8 (348)[a]
	Unpollinated	123	3.1 (7154)[b]	16.4 (214)[b]
Carson Pass	Cross-pollinated	54	77.6 (299)[a]	38.1 (225)[a]
	Self-pollinated	51	74.6 (292)[a]	38.3 (245)[a]
	Unpollinated	52	6.4 (6149)[b]	21.4 (310)[b]

> 0.80) (Table 2). Seed-set also did not differ between cross- and self-pollination (Table 2). Mean seed-set in fruits of cross-pollinated Table Mountain plants was not significantly higher than in self-pollinated fruits ($\chi^2 = 0.965$, P > 0.42). Seed-set did not differ between cross- and self-pollinated fruits of Carson Pass plants ($\chi^2 = 0.001$, P > 0.81), nor was the difference between populations significant ($\chi^2 = 1.716$, P > 0.25). Fruit-set of unpollinated flowers was significantly lower than for pollinated flowers ($\chi^2 = 66.481$, P < 0.0001), and seed-set for fruits of unpollinated flowers was significantly lower than for fruits of pollinated flowers ($\chi^2 = 13.352$, P < 0.0001).

Floral visitors. The most common and consistent flower visitors at *S. tortuosus* populations were bees, but a wide variety of insects foraged for pollen and nectar at all six study sites (see Appendix). The number and type of floral visitors differed among populations and among years (Table 3). In general, visitation rates were higher in plants at lower elevations, but otherwise there were no obvious patterns to the types or behaviors of floral visitors among the populations.

At Coulterville, *Bombus* species were the only visitors observed in 1985, although a few small solitary bees and a single *Apis mellifera* were captured on the flowers in 1984. In 1985, plants averaged 81.3 floral visitors per hour. At Table Mountain, *A. mellifera* was the principal floral visitor in 1984, 1985, and 1986, but was scarce in 1988. *Bombus* species were nearly the only visitors observed in late April 1988 and by mid-May still comprised 44.4% of the visitors. Other insects also visited the flowers, but usually in low numbers. I also observed a few visits by Anna's hummingbirds in the early part of the blooming peak (April). At Table Mountain, plants averaged 25.0 visitors per hour in 1985 and 55.9 visitors per hour in 1986.

TABLE 3. RELATIVE ABUNDANCE (PERCENT OBSERVED) OF FLORAL VISITORS IN 6 POPULATIONS OF *STREPTANTHUS TORTUOSUS*. * Present but not quantified in 1984.

Population	Year	*Bombus* spp.	*Apis mellifera*	All other bees	Wasps	Flies	Butter-flies
Table Mountain	1984	7.0	71.0	0.0	1.0	21.0	0.0
	1985	15.0	85.0	0.0	0.0	0.0	0.0
	1986	1.4	92.1	4.3	2.1	0.0	0.0
	1988	79.3	20.7	0.0	0.0	0.0	0.0
Coulterville	1985	99.3	0.3	0.6	0.0	0.0	0.0
	1984	100.0	0.0	0.0	0.0	0.0	0.0
Oregon Mountain	1984	*	*	*	0.0	0.0	*
	1985	43.6	0.0	50.0	1.8	0.0	4.5
Mount Shasta	1984	0.0	100.0	0.0	0.0	0.0	0.0
Carson Pass	1984	15.2	0.0	64.8	3.8	16.2	0.0
	1985	0.0	0.0	95.2	0.0	0.0	0.0
	1986	0.0	0.0	100.0	0.0	0.0	0.0
Tioga Pass	1984	57.5	0.0	27.8	0.0	13.8	0.0

Solitary bees, especially Megachilidae, were an important part of the pollinator fauna at Oregon Mountain, Carson Pass, and Tioga Pass. *Bombus* species and solitary bees were present in nearly equal numbers at Oregon Mountain in 1985. *Apis mellifera* was fairly common in 1984 but absent in 1985. I also observed the butterfly, *Euchloe hyantis,* visiting *S. tortuosus* for nectar as well as to oviposit on the leaves and flower buds. At Oregon Mountain, plants averaged 14.5 visitors per hour in 1985.

At Carson Pass, solitary bees were the most numerous visitors. In 1984, *Bombus* species were abundant, and I observed them foraging for pollen on various species and for nectar on *S. tortuosus.* In 1985 and 1986, however, I did not observe any *Bombus* species on *S. tortuosus.* Similarly in 1984, I found *Bombylius lancifer,* syrphid flies, and *Steniola tibialis* to be relatively abundant, but rarely observed them in 1985 or 1986. In 1985, plants averaged 7.6 floral visitors per hour, and in 1986, plants averaged 1.3 visitors per hour.

At Tioga Pass, *Bombus* species were the most frequent floral visitors, although I also found solitary bees and syrphid flies present. I did not observe *A. mellifera* at either Carson Pass or Tioga Pass, but during my 1984 visit to the Mount Shasta population, I observed *A. mellifera* visiting *S. tortuosus* flowers. No other bee species were observed at the Mount Shasta site, even on the other plant species present. Visitation rates at the Tioga Pass and Mount Shasta site were very low and were not quantified.

The behavior of floral visitors was similar in all populations. Within-plant visitors foraged on one to several racemes, typically working from the bottom of a raceme to the top, visiting 1–4 flowers. Visitors rarely handled every flower in a raceme. Nectar secretion began 1–2 days after the flowers opened, so all but the uppermost

flowers in a raceme were producing nectar. In 1985, I examined flowers in 133 racemes in the Table Mountain population (3.5 open flowers per raceme) and found that an average of 2.9 flowers were producing nectar.

Specimens of all bee species collected had *S. tortuosus* pollen on the face and mouthparts, and most had *S. tortuosus* pollen in the corbiculae. Syrphid flies and the small flower beetles also had *S. tortuosus* pollen on the mouthparts. No pollen was observed on the butterflies collected. Although the relative effectiveness of each species of floral visitors was not determined, the prevalence of bees as floral visitors indicates that bees are likely to be the principal pollinators. The small beetles were observed visiting flowers only during the staminate phase and are not likely to be pollinators.

DISCUSSION

Floral variation among populations of *S. tortuosus* does not appear to be explained by breeding system differences. Populations of *S. tortuosus* at high elevations do have relatively low visitation rates, yet there is no evidence of autogamy, and low levels of autofertility indicate that pollinators are required for normal seed set in both high and low elevation populations. Although pollen–ovule ratios were lower in higher elevation populations, they were still much higher than would be expected for a self-pollinating crucifer species (Preston 1986; Boaz et al. 1990).

Floral variation in *S. tortuosus* also could not be attributed to differing pollinator types or behaviors. Large-bodied bees were the principal floral visitors observed at the large-flowered Table Mountain and Coulterville populations, and small-bodied bees were the principal visitors at the smaller-flowered Carson Pass population. Large- and small-bodied bees, however, were almost equally common at the large-flowered Oregon Mountain population, and large-bodied bees were most common at the small-flowered Tioga Pass population. If my records of floral visitors to *S. tortuosus* flowers correspond to the actual pollinator fauna, then there is no discernible pattern that explains the floral variation.

The question of what has led to the extensive floral variation observed between populations of *Streptanthus tortuosus* remains unresolved. Traditional, pollination-based explanations for floral variation do not seem applicable.

During my work with *S. tortuosus*, I made numerous observations that suggest the course that future efforts should take to explain floral variation among populations. For example, flowers of *S. tortuosus* from Carson Pass develop more quickly than flowers of plants from Table Mountain, when grown in Davis (Preston 1991). Plants with smaller flowers may have an advantage at higher elevations if small

flowers develop more rapidly than large flowers. Rapid development improves the chances for high elevation plants to set and disperse seeds (Billings and Mooney 1968), and it has been shown that high elevation ecotypes develop and flower more quickly than low elevation ecotypes when grown together in a common garden (Clausen et al. 1948; Lawrence 1945; Ward 1969).

Another hypotheses may be that plants in high and low elevation populations differ in their pattern of resource allocation to flowering and fruiting due to a factor associated with elevation. Hall (1912) suggested that the shrubby habit of high elevation plants was due to suppression of the terminal raceme by frost damage to the apical meristem, and that small flower size was a consequence of producing many flowers. A focus on growth rates and allocation patterns between high elevation and low elevation populations, rather than on their pollination biology, will likely provide better clues to understand floral variation in *S. tortuosus*.

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APPENDIX

Visitors to *Streptanthus tortuosus* at six study sites in northern California during April, May and June 1984, 1985, 1986, and 1988; TM = Table Mountain (396 m); CV = Coulterville (548 m); OM = Oregon Mountain (762 m); MS = Mount Shasta (2316 m); CP = Carson Pass (2360 m); TP = Tioga Pass (2697 m).

COLEOPTERA: *Megilenthes* sp. (TM, OM, CP, TP); Dascillidae gen. sp. (OM).

DIPTERA: *Bombylius lancifer* O.S. (CP); *Eristalis nemorum* L. (CP); *Eristalis tenax* L. (TM); *Eupodes volucris* O.S. (TM, CP, TP); *Metasyrphus meadii* Jones (TM); *Metasyrphus lapponicus* Zetl. (CP); *Metasyrphus snowii* Wehr. (CP, TP); *Melanostoma latum* Curren (TP); *Melanostoma stegnum* Say (TP); 3 Syrphidae gen. sp. (TP).

HYMENOPTERA: *Ceratochrysis* sp. (OM); *Chrysura* sp. (CP); *Polistes fuscatus aurifera* Saurseure (TM); *Ammophila* sp. (TM); *Steniola tibialis* Handl. (CP); *Colletes* sp. (TP); *Dialictus* sp. (TM, CV); *Halictus* sp. 1 (CV); *Halictus* sp. 2 (OM); *Lasioglossum* sp. 1 (TM, OM, CP, TP); *Lasioglossum* sp. 2 (TP); 3 *Andrena* spp. (CP); *Anthidium mormonum* Cresson (TP); *Ashmeadiella* sp. (CP); *Chelostomopsis ribifloris* (Cockerell) (OM); *Dianthidium dubium* Schwartz (CV, OM); *Dianthidium pudicum* (Cresson) (CP); *Dianthidium heterulkei* Schwartz (CP, TP); *Hoplitis hypocrita* (Cockerell) (CV); *Hoplitis albifrons maura* (Cresson) (OM); *Hoplitis albifrons argentifrons* (Cresson) (CP); *Hoplitis fulgida platyura* (Cockerell) (CP); *Hoplitis* sp. 5 (CP); *Megachile melanophaea calogaster* Cockerell (TM, CP); *Osmia nemoris* Sandhouse (TM); *Osmia* sp. 2 (TM); *Osmia densa* Cresson (OM); 4 *Osmia* spp. (OM); 4 *Osmia* spp. (CP); 2 *Osmia* spp. (CP, TP); *Anthophora urbana* Cresson (TM, CP); *Ceratina* sp. (OM); *Xylocopa tabaniformis orpifex* Smith (OM); *Apis mellifera* L. (TM, CV, OM, MS); *Bombus edwardsii* Cresson (TM, CV, OM); *Bombus vandykei* (Frison) (TM, CV, OM); *Bombus vosnesenskii* Radoszkowski (TM, CV, OM); *Bombus flavifrons* Cresson (CP); *Bombus bifarius* Cresson (CP, TP); *Bombus sylvicola* Kirby (CP, TP); *Bombus centralis* Cresson (TP); *Psithyrus insularis* (F. Smith) (OM); *Psithyrus fernaldae* Franklin (TP).

LEPIDOPTERA: *Euchloe hylantis* (Edwards) (OM).

NOTEWORTHY COLLECTIONS

ARCTOSTAPHYLOS MEWUKKA Merriam subsp. MEWUKKA (ERICACEAE).—Mariposa Co., chaparral covered slopes above Merced River, Hwy 140, E of Briceberg, 530 m. T3S R18E, with *Adenostoma fasciculatum* and *Arctostaphylos viscida,* 15 Sept 1993, *J. Keeley & M. Keeley 25100* (LOC); chaparral 1 km W of Mt. Bullion, lower edge of chaparral belt, with *Adenostoma fasciculatum* and *Arctostaphylos viscida,* 650 m, 15 Sept 1993, *J. Keeley & M. Keeley 25108* (LOC); Tuolumne Co., Priest Grade, Hwy 120, <1 km W of Priest, 1 yr old burned chaparral with *Adenostoma fasciculatum, Arctostaphylos viscida* and *Heteromeles arbutifolia,* 690 m, 14 Sept 1993, *J. Keeley & M. Keeley 25086* (LOC).

Previous knowledge. Upper edge of chaparral and exposed ridges in coniferous forest above 800 m (P. V. Wells, *Arctostaphylos* in The Jepson Manual, University of California Press, Berkeley, 1993) or 830 m (K. A. Schierenbeck et al., Plant Systematics and Evolution 179:187, 1992), western Sierra Nevada. Burl-forming *A. mewukka* is widely considered to be restricted to an elevational band between the upper range of the non-sprouting chaparral taxon *A. viscida* and the lower range of the burl-forming coniferous taxon *A. patula.*

Significance. Extends elevational range in the central Sierra Nevada by nearly 300 m down into the lower margins of chamise chaparral. From southern Tuolumne Co. to central Mariposa Co. It appears that *A. mewukka* is a significant component of the low elevation chamise chaparral. Apparently it has been overlooked in this region because it co-occurs with the superficially similar white-leaved *A. viscida.* Indeed, I have traveled Priest Grade (Hwy 120) more than a dozen times without suspecting I was observing slopes dominated by two species of manzanita. This is due partly to the ease with which *A. viscida* recruits along roadcuts, thus making it accessible to botanists, in contrast to the *A. mewukka* embedded in nearly impenetrable chaparral. However, following a 1992 wildfire, the resprouting *A. mewukka* was readily exposed across the slopes. From a distance, *A. mewukka* is difficult to distinguish from *A. viscida* but there are subtle differences such as the more sprawling habit, larger leaves and slightly different hue.

This finding is significant for two reasons. It clarifies a long standing mystery as to why the chaparral of the central and southern Sierra Nevada lacked a resprouting manzanita; chaparral in the Coast Ranges, Transverse Ranges and Peninsular Ranges have at least one burl-forming *Arctostaphylos* taxon, co-occurring with non-sprouting taxa. In addition, the previously held notion that *A. mewukka* is restricted to an elevational belt between *A. viscida* and *A. patula* has been repeatedly cited as circumstantial evidence of its intermediacy between these taxa and supportive of its hybrid origin. The observations reported here make this argument less compelling although there are other more compelling reasons for this hypothesis (e.g., Schierenbeck et al. ibid).

—JON E. KEELEY and MELANIE BAER KEELEY, Department of Biology, Occidental College, Los Angeles, California 90041.

SCIRPUS PUMILUS Vahl. (CYPERACEAE).—Mono Co., White Mountains, Cottonwood Creek watershed, South Fork Cottonwood Creek 300 m upstream from its confluence with Poison Creek, T4S, R35E, SW¼ of NW¼ sect. 8, 9 July 1992, *D. W. Taylor 13017* (JEPS, CAS, RSA, RM, COLO, MO), 2877 m elevation, in dense turf codominated by *Carex douglasii, C. praegracilis, C. subnigricans, C. aurea, Muhlenbergia richardsonis* and *Juncus balticus,* associated with *Thalictrum alpinum, Platanthera hyperborea* and *Oxytropus deflexa* var. *sericea* (nomenclature follows J. Hickman

[ed.] The Jepson Manual—Higher Plants of California, University of California Press, Berkeley, California, 1993)

Significance. Second known locality in California (cf. R. Cranfill Cyperaceae, Pp. 1106–1149 *in* J. Hickman, op. cit.), and first verified record for the White Mountains (cf. J. Morefield, D. W. Taylor & M. DeDecker, Pp. 310–364 *in*: C. A. Hall & V. Doyle-Jones (eds.), Plant Biology of Eastern California, University of California, Los Angeles, California, 1988).

Major and Bamberg (Madroño 17:93–109, 1964) were the first to report a California station for *S. pumilus* in the Convict Creek drainage in the Sierra Nevada (40 mi/60 km to the west), where it is rare on boggy calcareous substrates (marble or calc-hornfels) at or above timberline in the Convict Creek basin (R. Pemble, Ph.D. Dissertation, University of California, Davis, California, 1970).

In the White Mountains, *S. pumilus* occurs on the lower elevation edge of a large mass of Reed dolomite (K. B. Krauskopf, U.S. Geological Survey Map GQ-960, 1971), in basic soils (pH 8.1–8.3), a setting ecologically analogous to the single other California occurrence in the Sierra Nevada. The White Mountain occurrence of *S. pumilus* was first observed in 1977 (cf. T. Keeler-Wolf 1990, U.S.D.A. General Technical Report PSW-125, pp. 78–81). Voucher specimens were not immediately obtained, however, and shortly after discovery all flowering culms in the population were grazed by cattle. Subsequent attempts to relocate plants in the intervening years were also thwarted by chronic overgrazing. In the late 1980s, grazing management at the site improved conditions, making voucher collection possible.

—DEAN W. TAYLOR, Jepson Herbarium, University of California, Berkeley, CA 94720.

IDAHO

PIPTATHERUM MICRANTHUM (Trin. and Rupr.) Barkworth (POACEAE).—Clark Co., BLM land directly E of Birch Creek Campground, ca. 2.5 km SE of Blue Dome, T9N R30E S4 NW¼, elev. 1938 m, ca. 20 plants in cracks and ledges in deep alcove of limestone cliffs, no associated species, 10 August 1991, *R. Moseley 2435* (ID).

Significance. First report for Idaho. Searches of regional herbaria (CIC, ID, IDS, MONT, MONTU, UC, WS, and WTU) support this as a new state record and a range extension of ca. 100 km south and west from Beaverhead Co., Montana (*Ryerson 823* MONT). Intensive collection efforts in east central Idaho by the authors and students associated with ID have shown this to be the only known population in the state.

—ROBERT K. MOSELEY, Conservation Data Center, Idaho Department of Fish and Game, 600 S. Walnut St., Boise, ID 83707 and DOUGLASS HENDERSON, Department of Biological Sciences, University of Idaho, Moscow, ID 83843.

SPOROBOLUS ASPER (Michx.) Kunth (POACEAE).—Jerome Co., Federal land (Bureau of Reclamation withdrawal) 300 m downstream from bridge below Milner Dam, SE¼ SE¼ NW¼ of Section 29, T10S, R21E (114°01′11.0″W, 42°31′41.4″N), elev. 1244 m. Circa 100 plants in cracks of basalt terrace of north bank of Snake River, with *Sporobolus cryptandrus, Poa compressa,* and *Bromus tectorum,* and nearby in shallow stony sandy loam (pH 7.0), with *Juniperus scopulorum, Oryzopsis hymenoides, Stipa comata, Aristida purpurea, Bromus tectorum, Poa secunda,* and *Gutierrezia sarothrae*; 16 Feb 1992, *S. Popovich 1898* BLM-Shoshone, *S. Popovich 1899* RM; 5 Aug 1992, *S. Popovich 2000* ID, RM.

Significance. First verified report for Idaho and only known state population. Her-

baria searched were: BOIS, CAS/DS, CIC, G, ID, IDF, IDS, IFGH, MIN, MO, MONT, MONTU, NSMC, RENO, RM, RSA/POM, SRP, UC, UNLV, UTC, WS, and WTU. Personal communication with local authorities and announcements at 1992, 1993, and 1994 Idaho rare plant conferences resulted in no additional information. In 1977 Riggins (Iowa State Journal of Research 51:287–321) indicated one location in Idaho in a distribution map, but without a specimen citation. We have been unable to locate a voucher specimen. Field surveys in potential habitat along the Snake River corridor from Milner Dam to Bliss revealed no additional populations. Closest known populations are in eastern Oregon and Washington, where rare.

—Steve J. Popovich, Shoshone District, Bureau of Land Management, 400 West F Street, Shoshone, ID 83352 and Douglass Henderson, Department of Biological Sciences, University of Idaho, Moscow, ID 83844-3051.

ANNOUNCEMENT

A Symposium Sponsored by the
Friends of the Jepson Herbarium

The Future of California Floristics and Systematics:
Research, Education, and Conservation
3–5 June 1994
Valley Life Sciences Building, University of California, Berkeley

Friday, 3 June
  Reception/Welcome
  Talk: History of Berkeley Botany and the Jepson Herbarium, Lincoln Constance
Saturday, 4 June
  Morning Symposium
    Future of Plant Systematics, Science, and Society, Brent Mishler
    Flowers in the Garden: What Next for California Floristics?, Dieter Wilken
    Cooperation And Collaboration: Herbaria And Botanical Gardens, George Rogers
    Rarity in California, Peggy Fiedler
  Afternoon Workshops (concurrent)
    Threats to the California Flora; Collecting Guidelines and Documentation Technique; California Native Plant Society; How to Use the Jepson Manual; The Use of California Natives in the Landscape; Botanical Transect: Bodega Bay to Vacaville; Agency Activities; Computer Options for Systematics
  Dinner and Evening Talk: Peter Raven
Sunday, 5 June
  Field Trips

  Symposium papers will be published in a forthcoming issue of Madroño.

  For detailed information on registration and activities write to: Friends of the Jepson Herbarium, University of California, Berkeley, CA 94720.

REVIEWS

Flora of North America North of Mexico. Volume I: Introduction. Edited by Flora of North America Editorial Committee. 1993. Oxford University Press, New York, xxi plus 372 pages. $60, ISBN 0-19-505713-9 (v. I).

I expect John Torrey and Asa Gray shouted from the rooftops when Volumes I and II of the *Flora of North America North of Mexico* appeared in print late last fall, 1993. It is, after all, the beginning of the culmination of more than 160 years of botanical exploration, documentation, and analysis of the flora of the North American continent. However, the advent of this publication is not merely just the commencement of a 14-volume series of botanical nomenclature, taxonomy and phytogeography of a not insignificant portion of the western hemisphere. Nor will this publication in its entirety merely represent the end-product of an unfathomable amount of work by three generations of lay and professional botanists. The appearance of the *Flora of North America* is the clear expression of the continuing fascination of the evolution of the North American continent and its associated biota by an extraordinarily articulate cadre of scientists. I should think that Torrey and Gray would be bustin' proud.

The Flora of North America project began in 1965 following the Tenth International Botanical Congress in Edinburgh and the publication of Volume 1 of *Flora Europea.* But the initial attempts to produce a comprehensive flora for the North American continent floundered when the Smithsonian Institution and the National Science Foundation withdrew logistical and financial support in 1973. The project was reborn nine years later in 1982, and the Flora of North America (FNA) project now emanates primarily from the Missouri Botanical Garden. Eleven years after its rebirth, Volume I (reviewed below) and Volume II (Pteridophytes and Gymnosperms) were published.

Volume I consists of 15 essays collected into five parts. The volume begins initially with an introduction and history of the Flora of North America project, written by the principals Nancy Morin and Richard Spellenberg. This is an interesting essay on how the FNA project began, and why and where it is today. Part I, Physical Setting, contains a chapter on the climate and physiography by Luc Brouillet and David Whetstone (Chapter 1), and a chapter on soils by D. Steila (Chapter 2). Both are concise and clearly written discussions, in general well-illustrated by appropriate figures and tables. Some figures are a bit hard to decipher, as the more complex gray tones are not easily distinguishable from each other. For example, in Figure 1.11, differences in the major formations of bedrock geology are not clear, and this again is a problem in Figure 1.13 where physiographic provinces of North America are distinguishable only by name and not by symbol in the figure legend. This general lack of resolution does not seriously impair an otherwise extremely informative pair of articles.

What was clear from the reading of the first several chapters was the easy transitions from one chapter to the next. In essence, this volume does not suffer the fate of many other multi-authored texts, where variations in writing style and expression by different authors becomes bothersome to read in one sitting. Instead, the writing throughout Volume 1 is clear, elegant prose, and the Flora of North America Editorial Committee should be commended for the careful and consistent editing. I was hard-pressed to find even a typographical, much less grammatical, error.

Part II also contains two articles, Chapter 3 by Alan Graham on the history of the North American vegetation during the Late Cretaceous and Tertiary periods, and Chapter 4 by Paul and Hazel Delcourt on the paleological aspects of the climates and floras during the Late Quaternary. These are straight forward articles, and I found the extensive illustrations and explanatory captions extremely helpful. Those without a firm grasp of the geological history of our continent will be rewarded in spending time with this pair of articles.

Part III is the third duet of essays. Michael Barbour and Norman Christensen write about the contemporary vegetation (Chapter 5) and Robert Thorne discusses the phytogeographic patterns of North America (Chapter 6). I particularly liked Barbour and Christensen's explicit statement of the themes of their text, and that the article's organization included not just an overview of the major biomes, but also the regional variants. This format emphasizes the richness of our flora, as well as its distinctive organizational expressions. Photographs of the various vegetation zones range from adequate to excellent, but the purpose of illustration is always met, regardless. Some also might be a bit frustrated with a nomenclature in Chapter 5 that follows Munz (1968), not Hickman (1993) (e.g., *Stipa pulchra* = *Nassella pulchra, Rhus diversiloba* = *Toxicodendron diversilobum*), but such is the nature of botanical inquiry.

My favorite chapter was to be found in Part IV: Humankind and the Flora. In a characteristically perspicacious chapter entitled "Taxonomic botany and floristics," (Chapter 7), James Reveal and James Pringle bring our botanical heroes to life. This chapter is a wonderful tour through the history of botanical discovery in North America. I do not believe that anyone is left out, and the great number of photographs of the various personalities provides additional insight into each botanist. One can't help but pour over this essay and delight in putting a face to the detailed escapades of our botanical notables. Reveal and Pringle have written a delightful text.

Part IV of Volume 1 includes three other essays: Weeds by Ron Stuckey and Theodore Barkley (Chapter 8), Ethnobotany and Economic Botany by Charles Heiser, Jr. (Chapter 9), and Plant Conservation by George Yatskievych and Richard Spellenberg (Chapter 10). Chapter 8 on weeds briefly summarizes our current knowledge about "biological" weeds, and illustrates that many of our conspicuous botanical members harken from afar. Chapter 9 on ethnobotany was rather disappointing, given the rich botanical and anthropological lore of the North American continent. The topic was treated routinely, with headings like "narcotics," "hallucinogens," "stimulants," and "alcoholic beverages" treated in no more than four paragraphs. Medicines were also given short shrift, and Table 9.1 on the production of important crops of Canada and the U.S. seems a bit out of place. Chapter 10 on plant conservation begins with a discussion on the rationale for conserving species, and ends with on-going efforts at plant conservation at several organizational scales. Although the Appendix 10.1 is included presumably to illustrate the various kinds of plants threatened with extinction, it belies the magnitude of the problem. Chapters 8, 9, and 10 are enhanced by superb pen-and-ink drawings by some of the botanical world's better illustrators.

The final part, Part V, of Volume 1 provides critical background into the philosophy and rationale of the floristic treatments to come. Chapter 11 on species and genus concepts is written by G. Ledyard Stebbins, and it is characteristically thorough. Stebbins draws heavily from California examples to illustrate his points, but his pragmatic review is not hampered by a California-centric bias. His treatment of the importance of polyploid and apomictic species is particularly noteworthy, and I was also pleased with his discussion of species concepts. Although necessarily brief, he advocates the acceptance of a broader approach suggested by others (e.g., Levin 1979; Mishler and Donoghue 1982; etc.). In his classically elegant way, Stebbins suggests that "Nature forces botanists to adopt a pluralistic species concept" (239).

Warren Wagner and Alan Smith outline the ferns and fern allies of Volume II (Chapter 12), as does James Eckenwalder for the gymnosperms of Volume II in Chapter 13. Wagner and Smith systematically discuss the morphology, habitats, ecology, geography and classification of the Pteridophytes, and conclude with a candid "We still don't know[!]" in response to the long-asked question regarding why some sterile fern hybrids have undergone chromosome doubling to restore fertility and others have not (266). Both chapters 12 and 13 are elegantly illustrated with one-half page figures of North American pteridophytes and gymnosperms.

Arthur Cronquist details his system of classification of flowering plants as adopted by the *Flora of North America* (Chapter 14), adopting current terminology (e.g., apomorphic vs. plesiomorphic characters) that serves to ground the *FNA* in current

thinking. I had hoped to learn why Cronquist did not accept the recent work by Dahlgren and his colleagues (Dahlgren et al. 1985) on the taxonomy of the Liliaceae sensu lato, but I did not gain new insight. Volume I concludes with James Reveal's overview of flowering plant families (Chapter 15). Chapter 15 subsequently is followed by the very useful Appendix 15.1, a table outlining the taxonomy of the flowering plants according to the Cronquist system as adopted by the *Flora of North America*. The final appendix, Appendix 15.2, provides a table illustrating the concordance of family names accepted by the major systems of flowering plant classification systems.

As is customary to note, there are some distractions in the volume, but they are truly minor. Some, for example, might object to the large-size format and the hefty nature of the volumes. These are not strictly field books, but neither do I abuse my floras. For example, I would not backpack into the Sierra with a single *FNA* volume in my pack, but I will carefully stash the *FNA* in the back of my car when travelling to Montana collecting *Calochortus*.

Others may think that Volume I is unnecessary to have, in that it does not contain any diagnostic keys. This is far from true, as this text provides critical background and synthesis for understanding the philosophy, botanical traditions and assumptions that guide the development of the *Flora of North America*. As stated so eloquently by Reveal and Pringle in Chapter 8: "Most who pick up this and the subsequent volumes will find the history of systematics and floristics on every page, for each plant name has a story to tell. Those who look into that story will find wonderful rewards and an even greater appreciation of systematics" (192). I would add that the history of systematics and floristics of North America provided in Volume I are essential to the understanding and appreciation of each page of this botanical opus.

My parents maintained an extraordinary library in their home, full of books primarily on world geography and art history. These oversized books were kept on the lower shelves, mostly because their size and weight dictated such a place. As a child I spent hours lying on the floor, perusing their books to gain some extra insight into my parents' personalities, especially as to what gave them great joy and why they were so proud to be a part of humanity. I shall do likewise, and keep these volumes of the *Flora of North America* (and those to come) on the lower shelves of my library so that my children will have the same unspoken opportunities as I.

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—PEGGY L. FIEDLER, Department of Biology, San Francisco State University, San Francisco State University, San Francisco, CA 94132.

A Natural History of California. (California Natural History Guides: 56). By ALLAN A. SCHOENHERR. 1992. University of California Press, Berkeley and Los Angeles. xi + 772 pages. $38.00, ISBN 0-520-06921-8 (hardcover).

Allan A. Schoenherr, Professor of Ecology at Fullerton College for more than thirty years, avid traveler, and active advocate of rational environmental policy has prepared this splendid text that will enable all readers to quickly acquire substantitive insight

into the ecology and natural history of all of California, or simply their favorite regions.

Mr. Schoenherr's brief introduction to California's natural regions apprises the reader as to the scope and organization of the book. A condensed, but lucid review of basic ecology follows, encompassing concepts of ecosystem structure, complexity and stability, flow of matter and energy, laws of thermodynamics, nutrient cycling, and trophic relationships. The author continues with considerable discourse on weather and climate, as influenced by latitude, continental location and local topography, and classifications of biotic communities. Basic geology is discussed, emphasizing the complexity of California's landscapes. The relationships of geology, soils topography and climate are discussed in the context of the evolution of biotic regions and consequent high diversity and endemism found in California. The introductory chapters provide a solid foundation for understanding the remaining chapters, and will be enjoyed by all, regardless of their prior knowledge or experience.

The heart of this book is organized around geographic regions, "using as a starting point the geomorphic provinces described by the California Division of Mines and Geology." The Sierra Nevada, for which Mr. Schoenherr displays copious intimate knowledge, and reverence, is discussed extensively in all of its aspects including geology, climate, and the diverse plants and animals of its several biotic zones. Although the author states that the treatment of plants and animals is in no way intended to be exhaustive, there is no shortage of information here. Conspicuous, interesting and distinctive species and their ecological roles are emphasized. A separate chapter is devoted to subalpine and alpine environments of Mountaintops of the Sierra Nevada, Klamath province Cascade Ranges, Great Basin, and the Transverse and Peninsular Ranges, wherein Mr. Schoenherr examines the insular nature of mountaintops, and then compares and contrasts the floral and faunal components of these isolated regions. Again, the author demonstrates intimate familiarity with the places he discusses.

In the chapter entitled Pacific Northwest Mountains, the Klamath Mountains and Cascade Ranges are treated in the same format as that for the Sierra Nevada. Similarly, the chapters following in order include: Coast Ranges; Cismontane Southern California (Transverse and Peninsular Ranges); Deserts (Great Basin, Mojave, Colorado); and, Great Central Valley. As with the introductory chapters, everyone will benefit from reading each chapter, regardless of their level of familiarity or fondness for a particular biotic region. The reason for this is that not only does Mr. Schoenherr develop a thorough overview of each region, but each chapter also contains little-known, curious, interesting, enigmatic, anecdotal, insightful, and sometimes inciteful information. Each chapter is supplemented with a listing of selected references.

Finally, two chapters are devoted to the ecology and natural history of the diverse habitats of Inland Waters and the Coastline. These chapters are a bonus for those readers whose biological experience is primarily terrestrial, especially since the level of treatment is nearly as extensive as that of the previous chapters. Mr. Schoenherr closes the last chapter with a section on California's Islands, therefore, everyone will be satisfied and no biotic regions and habitats are left untouched. In an Epilogue, Mr. Schoenherr deplores the failure of many Californians to appreciate the value and fragility of natural systems, and dedicates his book to a changing attitude toward protecting and restoring California's rich natural heritage.

The book contains 371 photographic figures and line drawings to illustrate important features and concepts. The reader may notice that many of the photographs as reproduced as a little too dark. Although this is not a major detraction, the author indicates that this will be corrected in a second printing. The sixteen color plates, each with multiple figures are top-quality. A few minor typographical and spelling errors were noted. Mr. Schoenherr utilizes standardized common and scientific names almost universally, however, some persons may take exception to certain nomenclature for plants and animals used in this book. If one will forgive a few slight nomenclatural deviations, then they will have no trouble assimilating the more important aspects of this book. Yet other readers might suggest that the scientific usefulness

of the book is diminished by the absence of literature citations in the body of the text. Those readers should consider that the book, already two-inches thick, would be considerably thicker, had this been done. Some readers may object to the occasional sprinkling of Mr. Schoenherr's philosophy and environmental ethic, but probably not those readers genuinely interested in California's natural environments.

Mr. Schoenherr has admirably fulfilled his objective to familiarize readers with this special place called California. It is apparent that this book was an immense undertaking, and no other single reference compares to it in terms of volume and informational content. After reading it, a person will be able to describe the climate, rocks, soil, plants, animals and biogeography of any area of California, and be able to explain how things got there and the ways in which they relate to each other. This book will foster appreciation for California's natural diversity, much of which is treatened. The breadth and depth of Mr. Schoenherr's writing makes this book essential reading for those of all interests and avocations, including experienced biologists, environmental professionals, students and naturalists.

—CARL WISHNER, 28328 Agoura Road, Agoura Hills, CA 91301.

Interface Between Ecology and Land Development in California. Edited by JON E. KEELEY. 1993. Southern California Academy of Sciences, Los Angeles. 297 pages. $28, ISBN 0-9626305-3-5 (hardcover).

In the preface to this book, Jon Keeley comments that "The interface between ecology and land development is a battleground of opposing interests and values, with factions fighting to ensure their own version of quality of life." The symposium from which this volume arose was convened to provide a forum which would bring together researchers, policy makers, conservationists and other interested parties and which would explore strategies to deal with the inherent battle between ecology and development. The resulting proceedings consists of 49 papers on a wide variety of topics, grouped under headings "Biodiversity and conservation," "Land management and land stewardship," "Wildlife and corridors," and "Mitigation and community restoration."

The book starts off with a keynote address on "Ecology and species extinction: a global perspective," by Peter Raven, which provides one of the most coherently-argued and well written essays on the value of biodiversity and the problems facing it that I have come across. Raven firmly asserts that the root cause of the current biodiversity crisis is the rapidly increasing human population, but also points to the failure of the United States to assess its own population increase or its per capita consumption. These problems are central to the question of development in California.

The remaining papers are written by people from a variety of backgrounds: academic biologists, consultants, state and local government personnel and representatives of a variety of conservation interest and lobby groups. Given such a range of backgrounds, it is inevitable that individual contributions will push particular barrows, and that a certain level of distrust and/or cynicism will come through. However, the overall tenor of the volume indicates the need for the various groups to work together if anything of lasting value is to be achieved. In particular, there is a strong call for scientists to become more involved in policy and advocacy. Scientists traditionally sit on the fence when faced with contentious issues, partly out of self-preservation, but also because they are reluctant to make "bottom line" statements in the face of complexity and uncertainty. However, there is a growing recognition that planning and management decisions are going to be made anyway, and it is better that they are made with some scientific input instead of in a knowledge vacuum. Dan Silver summed the situation up nicely: "Activism and advocacy in politics and conservation are simply a necessity, especially for scientists. If we are to save what's left of our nature in southern California, nobody will do it for us."

The volume is well produced and relatively free of typographical errors, although Parker's paper is missing the last half of the reference list. There is also no index, which could be a bit frustrating. The quality and content of the contributions vary enormously, and the book suffers somewhat from the emphasis in many papers on current contentious issues, often of a very local or transient nature. While these are the bread and butter of most conservation activities, they are usually ephemeral, and hence many of the issues raised in the 1992 conference are now out of date—e.g., Bartel's paper gives a pre-election viewpoint on the Endangered Species Act, Ross & Ross's paper on Mt Tamalpais contains an addendum which indicates that the problem they focussed on has now been largely resolved. While such contributions are still useful, they have a short shelf life. The value of many of the papers on local issues could also have been enhanced greatly by a consideration of their broader implications.

Despite this criticism there are many useful ideas and case studies in this volume. It contains material which will be of interest to anyone interested in conservation and land use issues, be they academics or practicioners. Case studies cited could be used as discussion papers for students at a variety of levels. Only a few papers left me completely cold—for instance, Cody's paper raking over the coals of the SLOSS debate left me asking "So what?" Many important questions were touched on throughout the volume. For instance, what should we be conserving—species, ecosystems, genes, communities? How do we deal with dynamic landscapes that operate on timescales longer than we are used to considering and much longer than the average political lifespan? How important are corridors? Is ecosystem restoration possible, and if so, what sort of ecosystem do we aim at—i.e., how do we define "natural?"

The book falls short of general conclusions on these topics. In fact, it would have benefitted greatly from a final paper which drew out these and other issues. In particular, I would have liked to see a discussion of the importance of considering ecological processes rather than ecosystems as static entities. For instance the papers by Parker and Ross & Ross provide an interesting contrast between a recognition of the importance of maintaining essential processes versus the desire to maintain the current status quo in a sort of embalmed limbo. Ross & Ross's paper considers the question of prescribed burning on Mt. Tamalpais and points out the potential risk to the plant species and communities there, but Parker also points out the essentially dynamic nature of vegetation, which implies that what is there today need not necessarily be there tomorrow. The recognition of the dynamic nature of natural ecosystems has profound implications for conservation management and policy. The question of what to do with flammable vegetation in built-up and suburban areas has also taken on a new perspective following the 1993 Los Angeles fires.

A further area of debate which could have been more fully explored was the difference in approach of various contributors to the ecology/development interface. Many contributors did, indeed, view it as a battleground, in which conservation is a constant war against development and mitigation is rife. An alternative viewpoint surfaced every so often which suggested that conservation could and should become more proactive, develop wider community support, and become part of the planning and development procedure. Indeed, I would argue that conservation must do this. Unless the community at large (and hence the majority of voters for politicians and consumers of the results of development) see the value in conserving natural ecosystems, conservation efforts will always be too little too late. Conservation has to become a way of life, not a side issue, if we want to conserve biodiversity in California, or anywhere else for that matter.

To the extent that this book contributes to the process of increasing communication between the different groups involved in conservation/development issues in California, it is certainly a step in the right direction. If California, with its renowned go—ahead attitudes and relative wealth, cannot get the balance between conservation and development right, then there is little hope for anywhere else.

—RICHARD J. HOBBS, CSIRO, Division of Wildlife & Ecology, LMB 4, PO Midland, WA 6056, Australia.

ANNOUNCEMENT

RANCHO SANTA ANA BOTANIC GARDEN

SOUTHWESTERN BOTANICAL SYSTEMATICS SYMPOSIUM

BEYOND PHYLOGENY: USES OF PHYLOGENETIC TREES

Rancho Santa Ana Botanic Garden proudly presents its 10th Annual Botanical Systematics Symposium on May 28th. The topic will be "Beyond Phylogeny: Uses of Phylogenetic Trees." The keynote speaker is **Dr. Warren H. Wagner,** Department of Biology, University of Michigan. Papers will be presented by **Dr. Aaron Liston,** Department of Botany and Plant Pathology, Oregon State University; **Dr. Jeff Doyle,** L. H. Bailey Hortorium, Cornell University; **Dr. Vicki A. Funk,** Department of Botany, Smithsonian Institution; **Dr. Spencer Barrett,** Department of Botany, University of Toronto; **Dr. Brent D. Mishler,** Department of Integrative Biology, University of California, Berkeley; **Dr. Jonathan Wendel,** Department of Botany, Iowa State University.

The cost to attend this symposium is $60.00 per participant ($45.00 for students). This fee includes the Friday evening social, boxed lunch and dinner on Saturday. To register please send your name, address and telephone number along with a check payable to:

Rancho Santa Ana Botanic Garden
Systematics Symposium
1500 North College Avenue
Claremont, California 91711

Be sure to register early as space is limited. For more information, please call (909) 625-8767, ext. 251.

ANNOUNCEMENT

California Botanical Society Graduate Student Meetings Awards for Best Paper

The 15th California Botanical Society Graduate Student Meeting was held at U. C. Davis on 19 February 1994. The Meetings are a medium through which graduate students in all disciplines of botany present ideas and results of their research. This year's meeting was attended by graduate students and faculty representing twenty academic institutions from California, Oregon and Nevada. The following graduate students were given awards for best paper in three categories:

PROPOSED RESEARCH

Julie Green, Rancho Santa Ana Botanic Garden
  Isozyme analysis of genetic variation in the endangered narrow endemic *Oenothera deltoides* ssp. *howellii* (Onagraceae)

RESEARCH IN PROGRESS (tie)

Kris Shanks, San Francisco State University
  A systematic study of the genus *Tricholoma* (Tricholomataceae) in California
Jennifer A. Dunne, San Francisco State University
  Effects of soil moisture availability on establishement of *Pseudotsuga menziesii* seedlings in chaparral

COMPLETED RESEARCH

Manuel Lerdau, Stanford University
  Ecological controls over monoterpene emissions from Douglas fir

ERRATUM

The following correction should be made in the L. H. Rieseberg et al. paper (Madroño 41:30–38):

The black dots adjacent to the photographs in Fig. 1 in the original paper were all 1–2 mm lower than the fragments they were supposed to indicate. They are shown correctly here.
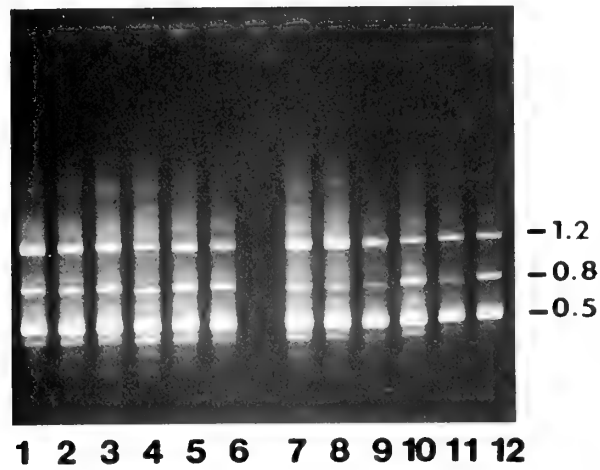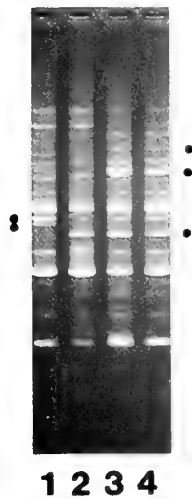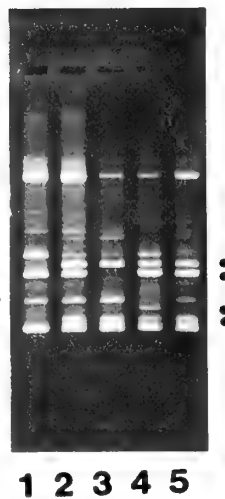
ANNOUNCEMENT

Annetta Carter Memorial Fund

Applications are solicited for modest grants to further botanical research in Baja California, Mexico. The Annetta Carter Memorial Fund, established in 1991, honors her for devoting the last 40 years of her life to the study of the Baja California flora (see Madroño 39:245–250). Her special interest included the floristics, history, biogeography, and ethnobotany of Sierra de la Giganta. In addition to several species that she discovered, the lovely rubiaceous shrub *Carterella alexandrae* was named in her honor, as has been the herbarium in La Paz and a street in Loreto.

The Fund has generated interest income to support two grants of $100 each. The grants are available to anyone conducting botanical research in Baja California. To apply send a 1–2 page proposal describing the goals and methods of the proposed project, and the proposed use of the funds. Include evidence that any permits or collaboration required will be obtained. Mail applications to the California Botanical Society, % University Herbarium, University of California, Berkeley, CA 94720. ***Deadline for proposals is 30 September 1994.***

Anyone wishing to make a donation to the Annetta Carter Memorial Fund may send a check to Holly Forbes, Treasurer, California Botanical Society, UC Botanic Garden, University of California, Berkeley, CA 94720. Please make checks payable to the *California Botanical Society,* with an indication that it is for the *Annetta Carter Fund.*

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members of the California Botanical Society, and membership is prerequisite for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or "erasable" paper. Avoid footnotes except to indicate address changes. Abbreviations should be used sparingly and only standard abbreviations will be accepted. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include a scale and latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used in MADROÑO 39(2). 1992. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th ed. Names of authors of scientific names should be abbreviated according to Brummitt and Powell, eds., *Authors of Plant Names* (1992, Royal Botanical Gardens, Kew) and, if not included in this index, spelled out in full. Titles of all periodicals, serials, and books should be given in full. Books should include the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

INVASIVE ALIEN PLANTS IN CALIFORNIA: 1993 SUMMARY AND COMPARISON WITH OTHER AREAS IN NORTH AMERICA

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Abstract

Publication of The Jepson Manual provides the opportunity to examine recent changes in California's alien flora. After accounting for inconsistencies we determined that The Manual reports 151 established alien species that were not included in any earlier statewide flora and eliminates 101 alien species that were included in one or more earlier statewide floras. The Manual and errata published in 1993 report a total of 1025 alien species in the state, which suggests the rate of alien species establishment has slowed during the last 25 or more years. Prior to this, the number of established alien plant species reported had grown exponentially since the time of European colonization. We list nine additional naturalizing aliens that have not yet been included in a statewide flora: *Amaranthus rudis, Catalpa bignonioides, Nerium oleander, Panicum texanum, Peganum harmala, Spartina anglica, Verbascum olympicum, Pinus halepensis, Pinus pinea*. The original (native) ranges of the "new" aliens differ slightly from those of earlier introductions; the majority are still of Eurasian origin but there has been an increase in the proportion of species introduced from North and Central America (about 15%) and from southern Africa (about 8%). The new introductions are not concentrated in one or a few areas. Instead, individual species sites-of-introduction are scattered throughout the state and in a variety of habitats. We also ascertained numbers and percentages of naturalized alien species from recently published floras for 37 other areas of North America and Hawaii. California has a higher number (1025) than any other area except New York state, which has 1082. California also has the fourth highest extrapolated mean number of alien species per 10 km² (182.2) of the areas analyzed but the percentage of the state's flora composed of aliens (ca 17.5%) is below that in 14 other areas.

Thaddaeus Haenke of Bohemia (now the Czech Republic) became the first academically trained botanist to explore California when he visited Monterey in the fall of 1791. Archibald Menzies, a British botanist, arrived the following year and explored more extensively (Cutter 1960; Presl 1973; McClintock 1989). The Jepson Manual–Higher Plants of California (Hickman et al. 1993), published just

TABLE 1. ALIEN SPECIES REPORTED IN THE JEPSON MANUAL FOR THE FIRST TIME. 151 species, 18 additional species mentioned *en passant* in the text only are In parentheses. + + indicates species positively known to have been in California more than 50 years ago, + indicates species which were very likely present in California more than 50 years ago, * indicates species which were very likely introduced to California within the past 50 years, ** indicates species which were very likely introduced to California within the past 25 years.

FERNS & FERN ALLIES

Pteridaceae: *Pteris tremula*

DICOTS

Aizoaceae: *Delosperma litorale*+, (*Disphyma australe*)

Anacardiaceae: *Pistacia atlantica*+ +, *Schinus terebinthifolius*+ +

Apiaceae: *Apium nodiflorum*+ +, *Hydrocotyle moschata, Oenanthe pimpinelloides*+ +, *Petroselinum crispum*

Apocynaceae: *Catharanthus roseus*

Asteraceae: *Arctotheca calendula**, *Artemisia annua, Carduus acanthoides**, *Carthamus eucocaulos,* (*Centaurea moschata*), *Centaurea × pratensis*+, *Chamaemelum nobile, Crepis bursifolia**, *Crupina vulgaris***, *Erechtites hieracifolia, Galinsoga quadriradiata, Heteranthemis viscidehirta, Leucanthemum maximum, Onopordum iliricum*

Boraginaceae: *Anchusa azurea,* (*Echium pininana*), (*E. strictum*), *Symphytum officinale**

Brassicaceae: *Alyssum desertorum, A. minus, A. strigosum, Aubrieta deltoidea, Cardamine hirsuta, Erucastrum galicum, Lepidium heterophyllum, Malcolmia africana, Sisymbrium erysimoides, S. loeselii, Teesdalia coronopifolia*

Callitrichaceae: *Callitriche stagnalis*

Caryophyllaceae: *Gypsophila elegans, G. scorzonerifolia, Moenchia erecta, Paronychia echinulata, Petrorhagia nantueilii, Stellaria pallida*

Chenopodiaceae: *Atriplex heterosperma, A. suberecta*

Cistaceae: *Cistus ladanifer, C. monspeliensis, C. salvifolius*

Convolvulaceae: *Ipomoea cairica*

Crassulaceae: *Aeonium arboreum, A. haworthii,* (*Crassula tetragona*)

Euphorbiaceae: *Euphorbia serrata**

Fabaceae: *Acacia baileyana*+ +, *A. cyclops, A. elata*+, *A. paradoxa*+ +, *A. pycnantha*+ +, *A. verticillata*+ +, *Aeschynomene rudis***, *Caesalpinia gilliesii, C. spinosa, Colutea arborescens, Cytisus multiflorus, C. striatus***, *Halimodendron halodendron**, *Onobrychis viciifolia**, (*Phaseolus lunatus*), (*P. vulgaris*), *Senna didimobotrya, Vicia lathyroides*

Geraniaceae: *Pelargonium panduriforme, P. quercifolium*

Hypericaceae: *Hypericum canariense*

Juglandaceae: *Juglans regia*+ +

Myoporaceae: *Myoporum laetum*+ +

Myrtaceae: *Eucalyptus citriodora*+ +, *E. cladocalyx*+ +, *E. pulverulenta,*+ + *E. sideroxylon*+ +, *E. viminalis*+ +, *Leptospermum laevigatum*+ +

Nymphaeaceae: *Nymphaea mexicana, N. odorata*

Onagraceae: *Epilobium leptophyllum, Oenothera biennis*

Oxalidaceae: (*Oxalis vallicola*)

Phytolaccaceae: (*Phytolacca heterotepela*)

Pittosporaceae: *Pittosporum crassifolium*+ +, *P. tenuifolium*+ +, *P. tobira*+ +, *P. undulatum*+ +, *Sollya heterophylla*+

Plumbaginaceae: *Limonium arborescens*

Polygonaceae: *Muehlenbeckia complexa, M. hastatula*

Primulaceae: (*Anagalis linifolia*)

Punicaceae: *Punica granatum*+ +

TABLE 1. CONTINUED.

Rosaceae: (*Acaena pallida*), (*Crataegus monogyna*), *Prunus cerasifera*++
Rubiaceae: *Crucianella angustifolia, Galium saxatile, G. schultesii, G. verum**
Sarraceniaceae: *Sarracenia purpurea**
Scrophulariaceae: *Bacopa monnieri*, B. repens, Mimulus ringens, Parentucellia latifolia, Pentstemon venustus, Verbascum speciosum**
Solanaceae: *Lycopersicon peruvianum*, (*Nicotiana alata*), (*Solanum mauritianum*)
Urticaceae: *Boehmeria nivea, Soleirolia soleirolii*
Verbenaceae: *Avicenia marina*, Lantana camara*++

MONOCOTS

Araceae: *Peltandra virginica*
Arecaceae: *Phoenix canariensis*++, *P. dactylifera*++
Commelinaceae: *Commelina benghalensis*
Cyperaceae: *Cyperus ligularis*, (*C. unioloides*), (*C. virens*), *Fimbristylis miliacea*++
Hydrocharitaceae: *Hydrilla verticillata*, Najas gracillima*
Iridaceae: *Gladiolus tristis, Ixia maculata, Sparaxis grandiflora, S. tricolor, Watsonia marginata*
Juncaceae: *Juncus cyperoides*+, *J. diffusissimus*
Liliaceae: *Allium paniculatum, A. vineale, Aloe saponaria* × *A. striata, Asparagus asparagoides, Muscari botryoides*
Poaceae: (*Ammophila breviligulata*), *Apera spica-venti*, Avena strigosa, A. sterilis, Brachypodium pinnatum, Bromus alopecurus, Cenchrus ciliaris, C. incertus, Echinochloa crus-pavonis, E. muricata, Eragrostis lehmanniana, Festuca trachyphylla, Nassella formicara [=Stipa formicarum], Panicum antidotale, Parapholis strigosa, Paspalum notatum, Piptochaetium setosum, Poa infirma*, (*Schizachyrium cirratum*), *S. scoparium, Spartina alterniflora**, S. densiflora, Ventenata dubia, Zizania palustris*
Pontederiaceae: *Heteranthera limosa**

over 200 years after these initial explorations, thus marks the beginning of the third century of study of the state's flora.

The Manual is an indispensable source of information on native vascular plant species and also provides up-to-date information on non-native, or alien, species growing without care in the state. With it we can examine how knowledge of the non-native flora has changed in the 25 years since the revision of the state's last comprehensive manual (Munz 1968). Questions we address below include: How many new alien species have been recognized as established in that time? Has the rate of alien species introduction changed? Are these newly introduced species from the same source areas as aliens that became established earlier? Where are these new aliens establishing in California? Is species richness of California's alien flora substantially higher than that of other areas in North America? Before we addressed these questions, however, we had to account for inconsistencies between the manuals (e.g., manuals differ on whether certain species are native or not, whether others have naturalized or only occasionally escape from cultivation, and whether certain taxa

merit species status). Details of this work are provided in an Appendix.

How Many Alien Species Have Been Recognized as Established in the Past 25 Years?

The Jepson Manual reports 1023 naturalized alien species in its Appendix I. Errata (Wilken 1993) added the Balsaminaceae with 2 alien species (*Impatiens balfourii* and *I. noli-tangere*) raising the total to 1025. After accounting for inconsistencies (see Appendix) we determined that The Manual includes 151 new alien species (Table 1) that had never been reported in earlier statewide floras. Eighteen more new aliens are also mentioned *en passant* in the text but not included among the 1025 naturalized aliens. Table 1 lists these species in parentheses.

We know of only eight alien species that have recently been reported in the literature as naturalizing in California but were not included in The Manual: *Amaranthus rudis* Sauer [*A. tamariscinus* misapplied] (Munz 1969), *Catalpa bignonioides* Walt. (Beauchamp 1986), *Nerium oleander* L. (Keeley 1992), *Panicum texanum* Buckl. (Fischer et al. 1985), *Peganum harmala* L. (Anonymous 1988), *Pinus halepensis* (McClintock et al. 1990), *Spartina anglica* C. E. Hubbard (Spicher and Josselyn 1985), *Verbascum olympicum* Boiss. (de Nevers 1985; this species is not from Greece, as many authors believe, but from the Bursa area in Anatolia—see Huber-Morath 1978). In addition, *Pinus pinea* L. was not included in The Manual, although it has naturalized and is spreading from plantation plantings on Santa Cruz Island (Steve Junak personal communication). Other species not included in The Jepson Manual but reported elsewhere as possibly naturalizing in California include: *Cassia artemisioides* Gaud.-Beaup. ex DC., *Cutandia memphitica* (Spreng.) Richt., *Cyperus papyrus* L., *Dichondra repens* Forst. & Forst., *Dodonaea viscosa* Jacq., *Dolichos lignosus* Pers., *Ficus pseudo-carica* Miq., and *Gleditsia triacanthos* L. (Beauchamp 1986; Munz 1974; Roberts 1989). *Cordyline australis* (Forst. f.) Endl. was reported naturalizing at Salt Point State Park (Sonoma County) by Ann Howald and Jake Sigg (personal communication). *Retama monosperma* (L.) Boiss [syn. *Genista monosperma* (L.) Lam.] has been reported naturalizing in and around Miramar Naval Air Station (San Diego County) by Michael Kelly (personal communication) and specimens have been deposited in DAV. Hybrids between *Raphanus sativus* and *R. raphanistrum* could be mentioned as well (see Panetsos and Baker 1967).

Has the Rate of Alien Plant Species Introductions Changed?

In order to examine trends in the establishment of alien species in California, the same criteria used for delimiting species and ad-

$$Y = a/(1+(b-1)e^{-cX})$$

Hickman et al. 1993

Munz 1968

Munz & Keck 1959

Estimates by
Frenkel (1970)

Jepson 1925

Brewer et al. 1876 & Watson 1880

1700   1750   1800   1850   1900   1950   2000   2050

Year

1600
1400
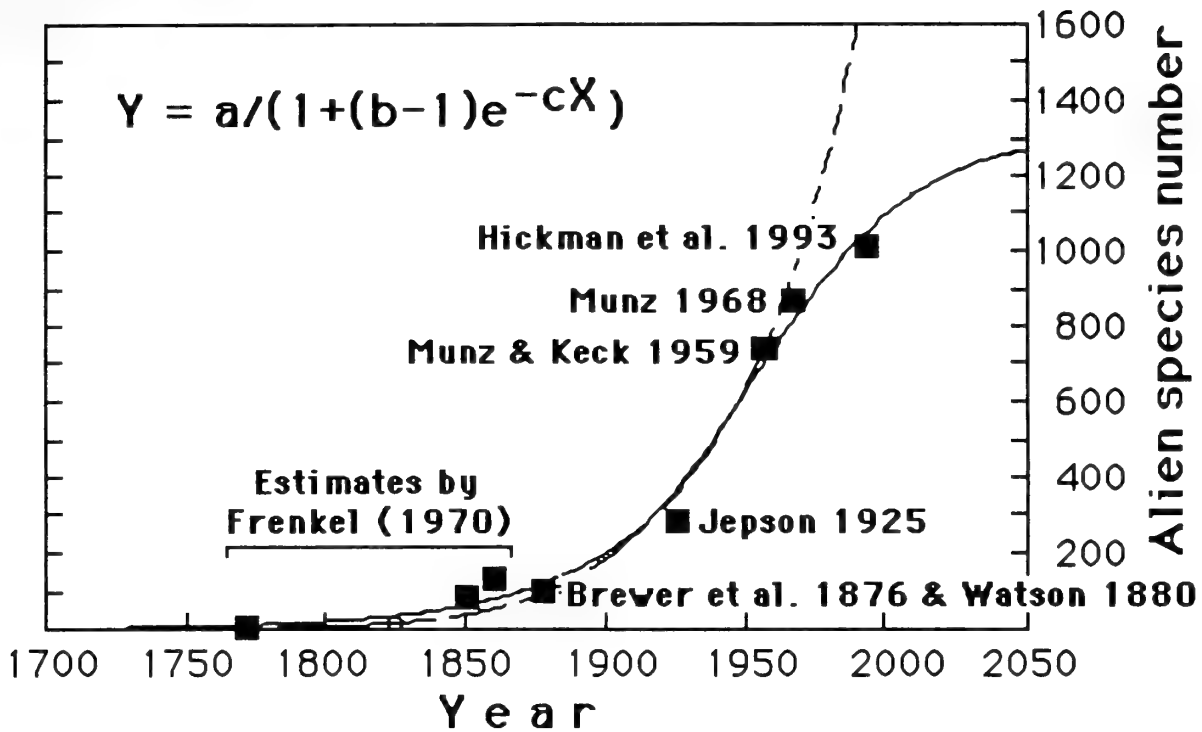1200
1000
800
600
400
200

Alien species number

FIG. 1.   Number of alien species of vascular plants in California flora during the period 1700–1993. Fitting the data by logistic function results in substantially different predictions depending on whether the last published number (1025; Hickman et al. 1993) is included (solid line) or not (dashed line).

mitting them to the flora in The Jepson Manual should be applied to the information in earlier Floras. To do this we considered alien species included in Munz and Keck (1959) and in Munz (1968) and eliminated those now considered native, those whose ability to naturalize has not been confirmed and those united into larger species in The Jepson Manual (see Appendix). Following this process the number of alien species included in Munz (1968) was 874 rather than 975 and the total in Munz and Keck (1959) was 725 rather than 797. Jepson's original Manual (Jepson 1925) recognized 292 alien species, and Brewer et al. (1876) and Watson (1880) recorded a total of 102 alien species in California. Estimates for earlier periods were published by Frenkel (1970).

The number of alien species reported in the California flora is plotted versus year in Figure 1. The data indicate that the rate of establishment of alien plant species has slowed during the last 25 or more years. A review of records at the California Department of Food and Agriculture (Rejmánek et al. 1991) supports this conclusion. Prior to this period, the number of established alien plant species reported in the state had grown exponentially with time since European colonization (Fig. 1). The logistic function $Y = a/(1 + (b - 1)e^{-cX})$ may be fitted to the data in Figure 1 and used to make predictions about numbers of alien species to be expected in the flora in the future. Not surprisingly, substantially different predictions result depending on whether the number of aliens reported in

1993 (1025) is included or not. Without this point, alien species numbers are predicted to continue increasing exponentially and R^2 does not differ whether exponential [$Y = ae^{bX}$] or logistic [$Y = a/(1 + (b - 1)e^{-cX})$] functions are used (0.995). When the point is included, however, use of the logistic function produces a slightly better fit ($R^2 = 0.993$) than the exponential function ($R^2 = 0.978$).

The rate of establishment of new aliens may have begun to slow far earlier than indicated in Figure 1. A species may be present and established, perhaps rapidly expanding its numbers and range, for several decades before it is collected and an acknowledgment of its presence published. Some of the 151 new alien species in The Jepson Manual were, in fact, present in California for a long time although they were not included in earlier Floras. *Fimbristylis milliacea* was first collected in California in 1866 but was not included in the flora until 1993! Similarly, *Juncus cyperoides* may have been introduced from Chile during the gold rush (Jokerst 1986). *Stellaria pallida* was previously not differentiated from *S. media* and *Heteranthemis viscidehirta* was previously reported as *Chrysanthemum segetum*. In addition, many decorative woody species that have been cultivated in the state for decades were recognized as naturalizing or occurring as waifs only recently (*Acacia* spp., *Catharanthus roseus*, *Caesalpinia* spp., *Cistus* spp., *Colutea arborescens*, *Eucalyptus* spp., *Lantana camara*, *Leptospermum laevigatum*, *Maclura pomifera*, *Myoporum laetum*, *Olea europaea*, *Phoenix* spp., *Pittosporum* spp., *Punica granatum*, *Schinus terebinthifolius*). *Pittosporum undulatum* was available in California by 1886 (Mack 1991). For other *Pittosporum* species see Eastwood (1932). For acacias cultivated 60 years ago see Jones (1933). For other alien woody species present at that time in California see Butterfield (1935), Graham and McMinn (1941), McMinn and Maino (1937), Saunders (1926), Walther (1928), and Wilson (1938).

It should be stressed, however, that while the rate of new introductions has likely slowed, many long-established aliens continue to expand their geographical ranges and influence in many habitats in California. Examples include *Abutilon theophrasti, Aegilops* spp., *Ageratina adenophora, Ammophila arenaria, Araujia sericofera, Arundo donax, Brachypodium distachyon, Cardaria* spp., *Carpobrotus edulis, Centaurea solstitialis, Chamaesyce serpens, Cirsium vulgare, Cortaderia jubata, Cynara cardunculus, Cyperus rotundus, Cytisus scoparius, Foeniculum vulgare, Gaura drummondii* (*G. odorata* misapplied), *Genista [Cytisus] monspessulana, Isatis tinctoria, Lepidium latifolium, Myriophyllum aquaticum, Pennisetum setaceum, Senecio mikanioides, Solanum lanceolatum, Tamarix ramosissima, Trifolium hirtum,* and *Ulex europaea*. The spread of many of these species is tracked by the California Department of Food and Agriculture (Barbe 1990) and the California Exotic Pest Plant Council (Newsletter published quarterly since 1993).

ARE THE NEWLY INTRODUCED SPECIES FROM THE SAME SOURCE AREAS AS ALIENS THAT BECAME ESTABLISHED EARLIER?

The information presented in The Jepson Manual on original (native) ranges of the new aliens indicates the source areas of these species are slightly different than those of earlier introductions. About 71% of the old aliens were from Eurasia and North Africa, 7% from North America, 1% from Central America (including Mexico), 9% from South America, 5% from southern Africa, 3% from Australia and New Zealand, and 3% from other parts of the world (Raven 1988; Rejmánek et al. 1991). If species assumed to have been in California for more than 50 years are excluded, the majority of the new aliens are still of Eurasian origin but the percentage is smaller, about 63%. At the same time, there has been an increase in the proportion of species introduced from North and Central America (about 15%) and from southern Africa (about 8%).

WHERE ARE THE NEW ALIENS ESTABLISHING IN CALIFORNIA?

Information in The Manual on the new alien species ranges in California indicates there have been changes in the sites of first establishment for aliens. Most of the old aliens first established at coastal sites near ports, the Spanish missions or early settlements, especially around San Francisco Bay, Los Angeles and adjacent areas of the south coast. The San Francisco Bay area and the south coast also support many of the new aliens. More impressive, however, is the fact that new alien species are present in all the major geographic subdivisions of the state outlined in The Manual (pp. 38–48). Some of the new introductions are already widespread but 27 have so far been reported from just one county. The geographic spread of these counties and the habitat types represented is also impressive: San Diego Co.; Los Angeles Co.; Ventura Co.; Santa Barbara Co.; San Luis Obispo Co.; Monterey Co.; Santa Clara Co.; Alameda Co.; Marin Co.; Sonoma Co.; Humboldt Co.; Riverside Co.; Inyo Co.; Stanislaus Co.; Placer Co.; Colusa Co.; Butte Co.; Plumas Co. and Lassen Co.

This spread of new introductions points to the great reach of modern human transportation systems. It also gives some indication of how difficult it will be to prevent further invasions since new introductions are no longer concentrated in a few areas where they could be easily monitored. Prevention of further invasions that could be disruptive economically and/or ecologically will therefore require greater vigilance throughout the state, perhaps including the use of screening techniques to prevent the entry of species with a high potential to become invasive (Rejmánek 1994).

TABLE 2. ESTABLISHED ALIEN VASCULAR PLANT SPECIES IN FLORAS OF NORTH AMERI-CA.* Corresponds to extrapolated mean number of alien species per 10 km². Boldface numbers indicate absolute numbers of alien species over 500, percentages over 20.0, and numbers of alien species/log(Area) over 90.0. † Pteridophytes not included. ‡ Numbers kindly provided by Dr. R. Mack. § Glacier-free area only. Sources: 1, Welsh (1974); 2, Taylor and MacBryde (1977); 3, Hickman (1993) and Wilken (1993); 4, Wiggins (1980); 5, Gould and Moran (1981); 6, Breedlove (1986); 7, Porsild and Cody (1980); 8, Moss and Packer (1983); 9, Lackschewitz (1991); 10, Welsh et al. (1987); 11, Martin and Hutchins (1980); 12, Gonzáles-Elizondo et al. (1991); 13, McGregor et al. (1991); 14, Johnston (1990); 15, Rzedowski and Rzedowski (1989); 16, Spellman et al. (1975); 17, Dwyer and Spellman (1981); 18, Morton and Venn (1990); 19, Mohlenbrock (1986); 20, Yatskievych and Turner (1990); 21, Wofford and Kral (1993); 22, MacRoberts (1984); 23, Dutton and Thomas (1991); 24, Gandhi and Thomas (1989); 25, Marie-Victorin (1964); 26, Rousseau (1971); 27, Senyour (1982); 28, Mitchell (1986); 29, Rhoades and McKinley (1993); 30, Harvill et al. (1986); 31, Radford et al. (1968); 32, Godfrey and Wooten (1979, 1981); 33, Cronquist (1980); 34, Wofford (1989); 35, Clewell (1985); 36, Wunderlin (1982); 37, Long and Lakela (1976); 38, Morton (1976); 39, LaRosa et al. (1992); 40, Whiteaker and Doren (1969); 41, Barret and Teeri (1973); 42 Böcher et al. (1978); 43, Bay (1993); 44, Rouleau and Lamoureux (1992); 45, Erskine et al. (1985), 46, Britton (1918); 47, Correll and Correll (1982); 48, Borhidi (1991); 49, Liogier and Martorell (1982); 50, Francis and Liogier (1991); 51, Wagner et al. (1990).

Region	Area (km²)	No. of native species	No. of alien species	Percent-age of alien species	No. of alien species per log (Area)*	Source
Alaska	1,530,700	1229	144	10.5	23.3	1
British Columbia	948,600	ca. 1900	**646**	ca. **25.4**	**108.1**	2
California	411,020	4844	**1025**	17.5	**182.6**	3
Baja California	143,700	2480	182	6.8	35.3	4, 5
Chiapas (Mex.)	74,211	ca. 6650	206	ca. 3.0	42.3	6
NW Territories	3,380,000	1055	53	4.8	8.1	7
Alberta	661,185	1475	280	16.0	48.1	8
Western Montana	7800	1251	250	16.7	64.2	9
Utah	219,883	2572	444	14.7	83.1	10
New Mexico	314,930	ca. 2680	229	ca. 7.9	41.6	11
Durango (Mex.)	123,181	ca. 3100	ca. 90	ca. 2.8	ca. 17.7	12
Great Plains	ca. 1,600,000	2495	394	13.6	63.5	13
Texas	692,397	4498	492	9.8	84.2	14
Valle de Mexico	7500	1910	161	7.8	41.5	15
Belize†	22,965	3023	107	3.4	24.5	16,17
Ontario	1,068,587	2056	**805**	**28.1**	**133.5**	18
Illinois	149,888	2058	**782**	**27.5**	**151.1**	19
Missouri	174,242	1920	**634**	**24.8**	**121.0**	20
Tennessee	109,150	2208	**507**	18.7	**100.6**	21
Louisiana	123,672	2580	405	13.6	79.5	22–24
Quebec	1,540,687	1803	**740**	**29.1**	**119.6**	25, 26
New England	172,676	1995	**877**	**30.5**	**167.5**	27
New York	137,795	1940	**1082**	**35.8**	**210.5**	28
Pennsylvania	119,316	2011	**969**	**32.5**	**190.9**	29
Virginia	105,570	2056‡	427‡	17.2	85.0	30
Carolinas	263,709	2890	436	13.1	80.4	31–34

TABLE 2. CONTINUED.

Florida Panhandle	38,628	1989	370	15.7	80.7	35
Central Florida	68,738	1746	440	**20.1**	**91.0**	36
Southern Florida	38,400	1259	ca. 400	ca. **24.1**	ca. 87.3	37–40
Devon Is. (Canada)	58,000	115	0	0	0	41
Greenland	326,000§	427	86	16.8	15.6	42,43
Newfoundland	144,890	906	292	**24.4**	56.6	44
Prince Edward Is-land	6650	624	316	**33.6**	84.2	45
Bermuda	54	165	303	**64.7**	**175.0**	46
Bahamas	14,500	1104	246	18.2	59.1	47
Cuba	114,525	5790	376	6.1	74.3	48
Puerto Rico	8897	2741	356	11.5	**90.1**	49,50
Hawaii†	16,764	956	**861**	**47.4**	**203.8**	51

How Does the Species Richness of California's Alien Flora Compare with That of Other Areas in North America?

Species richness of alien floras can be expressed in three different ways: (1) The total number of alien species, an interesting datum but one that is often positively correlated with the size of the area under investigation. (2) The percentage of alien species in the flora, a useful index but one that may be obscured by low or high richness of native flora. (3) The number of alien species/log(area), which can be used as a standardized expression of alien species richness because there is generally an approximately linear relationship between the number of species in an area and the log(area). When log to the base 10 is used, this index corresponds to the extrapolated mean number of alien species per 10 km². Nevertheless, it may yield a value far higher than the number of alien species that could be found in most 10 km² plots in the study area because it may be skewed by high densities of alien species typically found in coastal regions, cultivated areas and along rivers.

We present all three indices for California and 37 other areas in North America and Hawaii in Table 2. Species that are not established beyond cultivation or which have not been confirmed in this century were excluded. Resulting numbers of alien species are therefore often lower than those reported in the summary tables of the floras and checklists analyzed. New York is the only state with more reported naturalized alien species (1082) than California (1025). California also has the fourth highest extrapolated mean number of alien species per 10 km² (182.2) of the areas analysed. Nevertheless, the percentage of California's flora comprised by aliens (ca. 17.5%) is below that in 14 of the other areas examined.

A few trends are apparent in the data in Table 2. We will more

thoroughly explore these trends in another paper but outline them briefly here. The data are presented in the form of a series of 6 transects that run from north to south. On each transect the three indices tend to increase to a peak and then decline again from north to south. This is most clearly shown on the Pacific Coast (Alaska–Chiapas), Atlantic coast (Quebec–southern Florida) and Atlantic islands (Devon Island–Puerto Rico) transects and is weakest along the Ontario–Louisiana transect. Numbers of alien species decrease somewhat to the south of the peak regions but percentages of alien species generally decrease faster because native species diversity tends to increase with decreasing latitude. This trend is reversed in the region stretching from the Carolinas to southern Florida where there is a slight increase in the percentage of the flora composed of alien species and in the number of alien species/log(area) with decreasing latitude. On the other hand, the decline in aliens in Mexico is remarkable. Further evidence of this decline is presented in the Flora Novo–Galiciana (western Mexico), which reports only 6 aliens among the Asteraceae (McVaugh 1984). This represents a mere 0.8% of the region's Asteraceae while aliens account for 16.2% of the Asteraceae in California. All three indices of alien species richness are relatively low in the central and interior western North America floras analyzed (NW Territories–Durango and Great Plains–Belize transects) especially in comparison to areas on either coast.

The percentages of alien species in the Atlantic and Caribbean island floras examined followed a north–south trend much like that seen along the continental transects. The trend in numbers of alien species per log(area) is more complex with a second peak at its southern limit. Bermuda has the highest percentage of non-native species (64.7%) of any area we analyzed. This is more remarkable because the most recent flora for Bermuda was published in 1918 while the most recent floras used for the other 36 areas were published after 1970. Hawaii, which has the second highest percentage of alien species (47.4%) and the second highest number of alien species per log(area) (203.8) of all the areas we analyzed, has often been cited as an example of the special vulnerability of remote oceanic islands to alien species invasions.

Do these numbers indicate anything about regional differences in vulnerability to plant invasions? Or, do they reflect merely historical differences? Very likely both. Unfortunately, comparisons based on floras of whole states or groups of states can be misleading. Clearly, some of the diversity of California's alien flora may be explained by the state's tremendous topographic, climatic and edaphic diversity. On the other hand, this environmental diversity certainly contributes to the total number of native and especially endemic species and, therefore, to the relatively low percentage of aliens. Comparisons between smaller areas (counties, watersheds, mountain ranges

etc.) may be more fruitful. Such areas are, in general, more homogeneous, and causal connections between environmental factors, anthropic disturbance, history, and numbers of alien species may be more easily disentangled. Local floras that utilize standardized criteria for delineating species and classifying alien taxa as truly naturalized or not should serve this purpose. More analyses like those by Fiedler and Liedy (1987), Burgess et al. (1991), Poldini et al. (1991), DeFerrari and Naiman (1994), and Knops et al. (1994) are badly needed. Modern taxonomic treatments like the new Jepson Manual will be indispensable in such efforts.

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APPENDIX

A number of mistakes in The Jepson Manual's Appendix I (p. 1315) made it difficult to determine the numbers of native and alien species included within the Manual. Most of the errors were corrected in the *Errata to the first and second printings of the Jepson Manual* (Anonymous 1993). The corrected Appendix I states that "among the 5867 species known to occur in California, 3423 species (58.4%) are native to California and elsewhere in North America, 1416 species (24.2%) are endemic, and 1023 (17.4%) are naturalized aliens or waifs". Appendix I's table of MAJOR TAXONOMIC GROUPS was also corrected by properly labeling row four "additional subspecies or varieties" and adding a row with accurate figures for "endemic species". The only remaining problem we detected is that the first sentence of the revised version of Appendix I incorrectly states "*The Jepson Manual* includes descriptions of . . . 5862 species . . ." [elsewhere it is 5867]. The addition of the Balsaminaceae (Wilken 1993) brings the total number of species known in the state's flora to 5869 and the total number of aliens to 1025 as noted above.

The Jepson Manual's Appendix I defines alien taxa as those "believed to have been introduced from other parts of the world since the first European colonization and that have either become subsequently naturalized or are waifs." The total reported number of aliens (1025) is low relative to other tabulations (compare Rejmánek et al. 1991), however, which suggests that some waifs may have been excluded. In addition, the Glossary defines waifs as "alien (not native) and either not reproducing without human intervention or not persisting for more than a few generations and therefore incompletely naturalized. Most known waifs are not treated in The Jepson Manual." Despite this, a number of species that could easily be labeled waifs are described in the text (e.g., *Arctotis stoechadifolia, Bupleurum lancifolium, Chasmanthe floribunda, Juglans regia, Luma apiculata, Venidium fastuosum, Watsonia marginata,* some *Ipomoea, Oxalis,* and *Pittosporum* species). And in fact, some of the 1025 alien species described in the text and errata are labeled "waifs" by the Manual authors (e.g., *Amaranthus arenicola, A. deflexus, Anchusa azurea, Antirrhinum orontium, Aponogeton distachyon, Consolida ambigua, Kallstroemia grandiflora, Kickxia*

elatine, Lantana montevidensis, Linaria supina, Physalis viscosa, Ranunculus sardous, Salvia aethiops, Verbena tenuisecta). Part of this inconsistency is due to the fact that some species fall along the continuum between clearly naturalized species and waifs and might reasonably be classified as either. The resulting number, 1025, is therefore a mixture of clearly naturalized species and some waifs, as was true in previous floras (Munz and Keck 1959; Munz 1968).

The Jepson Manual's Appendix III lists name changes, additions and deletions to the flora that have occurred since the publication of earlier statewide references. It provides clear statements like "not naturalized" or "not clearly naturalized" for many of the alien species included in Munz and Keck (1959) and Munz (1968) but dropped from The Jepson Manual. Alien species that were not reported in older manuals but that are included in The Jepson Manual, are labeled as "naturalized" or "waif" in this list. This is helpful but, unfortunately, not consistent. For example, *Trifolium glomeratum, Ficus carica, Olea europaea, Polygonum pensylvanicum, Valerianella carinata, Calamagrostis incertus, Poa bulbosa*, and *Setaria faberi* are listed as additions although they were included in Munz's Floras. On the other hand, *Arctotheca calendula, Juncus cyperoides, J. diffusissimus*, and *Schizachyrium scoparium* are reported for the first time but are not listed in Appendix III. After accounting for these inconsistencies we determined that the Jepson Manual includes 151 new alien species.

Adding 151 new alien species to the 975 aliens reported in Munz's manuals (Rejmánek et al. 1991), yields a total of 1126 alien species, 101 more than reported in The Jepson Manual and 1993 errata. Therefore, we had to account for this discrepancy before continuing. Fates of the 101 alien species included in the flora earlier but not recognized in The Jepson Manual were diverse:

1. Some species previously classified as aliens are now considered native: *Draba verna, Eclipta alba (E. prostrata), Galium tricornutum, Lepidium virginicum, Lippia nodiflora, Madia sativa, Rorippa nasturtium-aquaticum, Sagina procumbens*. However, it is surprising that *Draba verna* is treated as a native and *D. nemorosa* as introduced. Patterns of their distribution (see maps 964 and 966 in Hulten and Fries 1986) and treatment in Rollins (1993) suggest the opposite. *Galium tricornutum* Dandy (*G. tricorne* Stokes p.p.) is described as a native but was certainly introduced from Europe (Dempster 1979). Native status for *Rorippa nasturtium-aquaticum (Nasturtium officinale)* is surprising; the author of the treatment was of different opinion some 10 years ago (Rollins 1981) and still seems to be (Rollins 1993). The status of *Sagina procumbens* is open to speculation (Crow 1978; Hulten and Fries 1986).

2. Most of the species labeled "not naturalized" in Appendix III were reported earlier but apparently were not confirmed recently (43 species). The exclusion of some of these species was suggested by Raven and Axelrod (1978) but the exclusion of others is not always justified. For example, *Lolium strictum* Presl (*L. rigidum* Gaudin ssp. *rigidum*) is excluded for lack of documentation (p. 1362), although California-collected specimens are in the Beecher Crampton Herbarium (AHUC). On the other hand, some questionable (*Apium nodiflorum, Halodule wrightii*), unconfirmed (*Acacia decurrens, A. mearnsii*), undocumented (*Caragana arborescens*), or "likely eradicated" species (*Halimodendron halodendron, Sarracenia purpurea, Sphaerophysa salsula*) are included in The Manual.

3. Some previously recognized small species are now united in larger species (e.g., *Bromus commutatus, Chenopodium opulifolium, Coreopsis atkinsoniana, Galium spurium, Mentha longifolia, Plantago rhodosperma, Rubus alamus, Rumex angiocarpus, Soliva daucifolia, Sorghum virgatum, Tamarix africana, Taraxacum laevigatum, Tolpis umbellata, Torilis heretophylla, Vicia angustifolia, V. dasycarpa*). *Bromus unioloides (B. haenkeanus)* and *B. willdenowii* are included in *B. catharticus*. *Hordeum glaucum (H. stebbinsii)* and *H. leporinum* are included in *H. murinum*. *Geranium microphyllum* and *G. pilosum* are included in *G. potentilloides*. Most of these changes are substantiated by recent literature although *Chenopodium opulifolium* and *Taraxacum laevigatum* are usually recognized as distinct species in floras

published in the past 5 years (Gleason and Cronquist 1991; Stace 1991; Tutin et al. 1993). Plants called *Rumex angiocarpus* in California could be treated as subspecies of *R. acetosella* (ssp. *pyrenaicus* (Pourret) Akeroyd). This subspecies with tepals not separable from the ripe achene may be more common in California than the nominal ssp. *acetosella,* especially at lower elevations.

4. A few species were previously reported from California by mistake or are undocumented: *Camelina sativa, Cuscuta suaveolens, Juncus sphaerocarpus, Malva verticillata, Opuntia megacantha, Polygonum aviculare, Setaria carnei, Torilis japonica, Trifolium procumbens, Verbena officinalis.* Most plants that have been called *Polygonum aviculare* in California seem to be another alien of European origin—*P. arenastrum* Boreau—a species recognized already by Munz (1968). This is interesting because in western and southern Europe, *P. aviculare* is reported as more common than *P. arenastrum* (Blamey and Brey-Wilson 1991; Raffaeli 1982; Stace 1991). The same is true for New Zealand where both species were introduced (Webb et al. 1988). However, it is questionable whether *P. aviculare* is really undocumented in California (see Mertens and Raven 1965; Wolf and McNeill 1987).

5. Four alien species reported in Munz's Floras are mentioned only briefly in the text of The Jepson Manual but not included among the 1025 "naturalized aliens" (*Brassica oleracea, Papaver dubium, P. hybridum, Ruta graveolens*).

6. Some alien species reported in Munz's Floras are never mentioned in The Jepson Manual (e.g., *Melampodium perfoliatum* [Asteraceae], *Pentaglotis sempervirens* [Boraginaceae], *Inopsidium acaule* [Brassicaceae], *Atriplex vesicaria* [Chenopodiaceae], *Sisyrinchium minus* [Iridaceae], *Hordeum distichon, H. vulgare* [Poaceae]). The genus names of other aliens reported in Munz's Floras are mentioned in The Jepson Manual's family treatments but the species themselves are not listed or described (e.g., *Cedronella canariensis* [Lamiaceae]). Presumably, all these species should be treated as those under '2' above.

LINANTHUS LATISECTUS (POLEMONIACEAE), A NEWLY DESCRIBED SPECIES FROM THE CALIFORNIA NORTH COAST RANGES

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ABSTRACT

Linanthus latisectus, a newly recognized species from the southern portion of the California North Coast Ranges, is most similar to *L. androsaceus* and *L. parviflorus* but is morphologically distinct from those species in having orbicular cotyledons, an inflorescence of few bracts, an intermediate-sized corolla that remains open after initial anthesis, a densely glandular-pubescent calyx with lobes connivent around the corolla tube, and leaves positioned at a 90° angle to the stem, with broad, recurved lobes that are commonly rounded at the apex.

In the course of assessing phenetic relationships among species in the *Linanthus androsaceus* complex (*L, androsaceus* (Benth.) Greene, *L. parviflorus* (Benth.) Greene, *L. bicolor* (Nutt.) Greene, *L. acicularis* Greene, and *L. serrulatus* Greene) in sect. *Leptosiphon* (Endl.) V. E. Grant (Grant 1959), the existence of an undescribed morphological entity became evident. Analysis of character states in specimens from field collections made in Sonoma, Lake, and Mendocino Cos., employing multivariate statistical methods (Multidimensional Scaling, Cluster Analysis, and Discriminant Function Analysis) (Buxton 1993), revealed a discontinuity in the pattern of variation of several characters. Extensive field observations and a survey of herbarium specimens from surrounding counties corroborated the results. The rationale for specific recognition of this entity is consistent with taxonomic concepts used in treatments of *Linanthus* and other genera in Polemoniaceae.

Linanthus latisectus E. Buxton, sp. nov. (Fig. 1).—TYPE: USA, California, Mendocino Co., Tomki Road, 2.1 km N of junction with Canyon Road (Mendocino Co. Road 308) on west-facing roadbank, elev. 415 m, 3 May 1992, *E. Buxton 975* (holotype CAS; isotypes JEPS, MO, NCC, RSA, SFSU, US).

Inflorescentia bracteis paucis; cotyledones orbiculatae; folia ad angulum 90° patentia, 3–5(7) lobata, dense ciliata, lobi decurvati, apices plerumque rotundati, lobi medii usque ad 3.5 mm lati; calyx extus dense pubescens et glandulosus usque ad apices loborum, trichomata circa 1 mm longa, lobi tubum corallae conniventes, folia
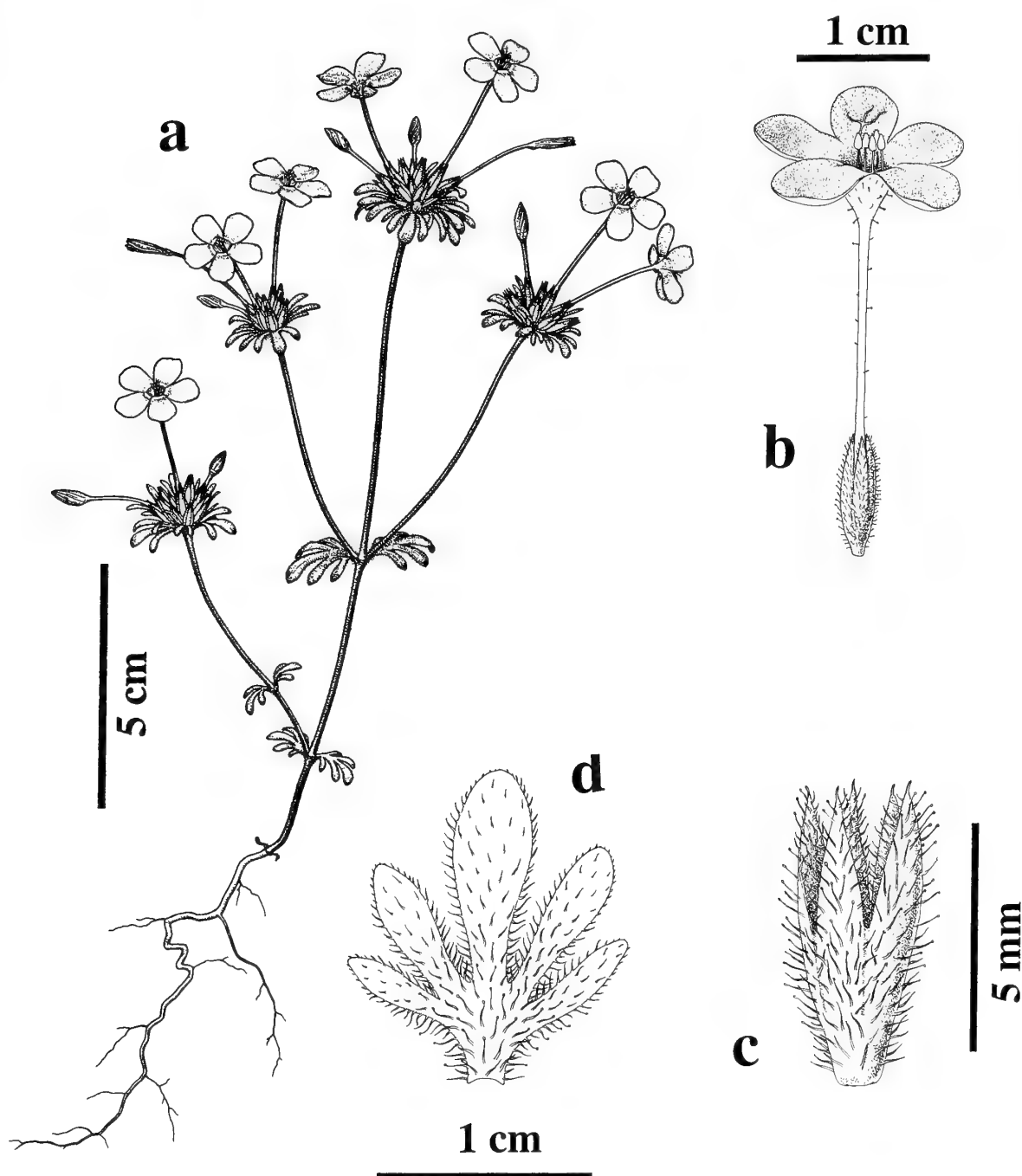
FIG. 1. *Linanthus latisectus* E. Buxton. **a**, habit illustrating leaf blade/stem angle and recurved leaf lobes. **b**, corolla with calyx lobes connivent around tube. **c**, calyx with glandular trichomes. **d**, leaf.

et calyces colore veneto; corolla 14–18 mm diametro, lobi plerumque obovati, atrorosei, raro albi, faucibus omnino flavis, post apertionem nunquam clausa usque ad senectutem.

Annual herb; herbage commonly bluish green. Cotyledons orbicular. Primary tap root with lateral roots extending to about one meter in loose soil. Stems erect or slightly decumbent, wiry, simple, or branched above and below, 7–20 cm high, pubescent with appressed to slightly spreading trichomes. Leaves opposite, palmately to pinnate-palmately divided, commonly somewhat succulent, un-

divided portion of leaf blade at right angle to stem, lobes recurved, middle lobe obovate to broadly spatulate, frequently rounded at apex, 2–3.5 mm wide; leaves subtending inflorescence 3–5(7) lobed, middle lobe 6.5–9.5 mm long, undivided portion of leaf blade 3–6 mm long, adaxial surface moderately to densely pubescent, abaxial surface frequently glandular-pubescent, marginal trichomes soft, dense, ca. 1 mm long; leaves at internode immediately below inflorescence (3)5–7 lobed, middle lobe 6–8 mm long, lateral lobes frequently curved toward middle lobe, undivided portion of leaf blade 2–4 mm long, slightly less pubescent than that subtending inflorescence. Calyx 5–8 mm long, 5–lobed with a narrow hyaline membrane below sinuses, lobes 2.5–4.5 mm long, densely glandular–pubescent to tip, ciliate trichomes dense, ca. 1 mm long, tips of calyx lobes connivent around corolla tube. Flowers sessile in terminal, many- to few-flowered heads with few bracts, 2–4(5) flowers open at a time. Corolla salverform, limb 14–18 mm in diameter, lobes broadly oval to obovate, commonly truncate, occasionally cuspidate, predominantly reddish pink (rarely light pink or white), tinged abaxially with white; corolla rarely closing after initial anthesis until senescence. Corolla tube 17–26 mm long, ca. 1 mm wide, glabrous to slightly glandular-puberulent, red to purple. Throat short, 1–1.5 mm long, internally dark yellow with a white border, occasionally with narrow dark lines perpendicular to radius of limb, externally slightly glandular-pubescent. Filaments inserted at top of tube, ca. 2 mm long, slightly flattened. Anthers exceeding throat, forming a column before dehiscence, then commonly versatile. Style exserted, mostly just beyond anthers. Stigmata 1.5–2.5 mm long, occasionally longer, slightly flattened, orange. Capsule obovoid, 3–locular with several seeds per locule. Seeds 1–1.25 mm long, lenticular or angular, corrugated, yellowish tan, mucilaginous when wet.

Paratypes. USA, California: Glenn Co., W of Bennett, *Heller 11993* (CAS); Humboldt Co., Dinsmore's, *Eastwood 4764* (CAS); NE of Garberville, *Cantelow 4125* (CAS); Bell Springs Rd. between Bell Springs and Blue Rock Ranch, *Sharsmith 4383* (UC); Lake Co., Serpentine Hill, 1 mi. S of Lakeport, *Baker 9563* (NCC); Middle Creek above Upper Lake, *Eastwood 5662* (CAS); New Potter Valley, *Cantelow s.n.* (CAS); Summit to Bartlett Springs, *Abrams 12453* (CAS); Putah Creek, SW of Lower Lake, *Constance 2140* (WS); 1 mi. S of Lower Dam, Eel River, *Wiggins 12108* (UC); E side of Bartlett Mtn., *Mason 11095* (UC); Mendocino Co., Near beginning of Outlet Creek, N of Willits, *Baker 9931* (UC); Red Mountain N just below summit, *Smith 6921* (CAS); 4 mi. N of Rockport, *Breedlove 2983* (CAS); Near Bell Springs, *Eastwood 4608* (CAS); 7 mi. S of Willits, *Wiggins 10196* (WS); Rd. to Eden Valley, W of summit, *Nelson 895* (WS); Mt. Sanhedrin, *Bacigalupi 1534* (UC); Potter Val-

ley, *Eastwood 12725* (CAS); Middle Fork, Eel River, 6 mi. SW of
confluence w. Black Butte River, *Wheeler 1478* (CAS); Hopland
to Cloverdale, *Abrams 7032* (CAS); Potter Valley Rd. to Lake Pills-
bury, *Cantelow 4129* (CAS); Ukiah, *Kellogg 822* (CAS); Leonard
Lake, *Smith 5779* (CAS); Hwy. 101, 12.7 mi. SE of Laytonville,
Lenz s.n. (UC); Longvale, *Howell 1311* (CAS); 7.8 mi. W of Ukiah,
Low Gap Rd., *Cantelow s.n.* (CAS); Wilderness Rd., 1.6 km N of
jct. w. Route 429, *Smith 5391* (CAS); Sherwood Rd., W of Willits,
Smith 6594 (CAS); 7 mi. E of Willits, *Barneby 11575* (CAS). Shasta
Co., Baird, *Howell 1829* (CAS); Kennett, *Smith 169* (CAS); Near
Redding, *Heller s.n.* (CAS); Pitt River, near Hermett, *Smith 16*
(CAS); Antler Campground near Lakehead, *Thiers 27367* (SFSU);
Lakeshore Dr. at Antler Rd., *Vagenas 108* (SFSU); Sonoma Co.,
Cavedale Rd. 3.6 mi. NE of Hwy. 12, *Ammirati 61* (SFSU); Sonoma
Mtn. near origin Matanza Creek, *Hillard 5* (SFSU); Pepperwood
Ranch, *Buxton 946* (CAS); Santa Rosa Creek Canyon, *Baker 5143*
(NCC); Tehama Co., Hwy. 36, 5 mi. E of Redbluff, *Ahart s.n.* (CAS);
W of Plaskenta between 9 & 10 mi. posts, *Baker 12616* (UC); Trinity
Co., 1 mi. S of Zenia on Covelo Rd., *Wolf s.n.* (CAS).

Distribution. Linanthus latisectus occurs in the California North
Coast Ranges at elevations from 170 to 1500 m from east Central
Sonoma Co., throughout Lake and Mendocino Cos., and into Hum-
boldt, Glenn, Tehama, Shasta, and Trinity Cos. Its center of distri-
bution appears to be Mendocino and Lake Cos.

Habitat and phenology. Linanthus latisectus occurs on hillsides
and steep (to 45°) roadcuts in soils derived from marine sediments
of the Franciscan Complex, and occasionally on serpentine. It com-
monly grows in mixed evergreen forest communities with *Quercus
kelloggii, Q. garryana, Arbutus menziesii, Pseudotsuga menziesii,
Arctostaphylos* spp., *Ceanothus integerrimus, Toxicodendron diver-
silobum,* and *Rhamnus californica.* It grows in leaf litter, or inter-
mixed with various forbs and grasses including *Lotus humistratus,
Eriophyllum lanatum, Lupinus nanus, Platystemon californicus,
Calochortus amabilis, Triteleia laxa, Bromus hordeaceus,* and *Ely-
mus glaucus.* It also occurs in open, barren places on unstable, sandy
to gravelly soil with few associated species. The flowering period of
L. latisectus extends from late April through June, depending on
elevation and latitude.

Relationships and morphology. Section *Leptosiphon,* one of six
Linanthus sections (Grant 1959), comprises ten annual species with
the center of distribution in California. The species in this section
are characterized by sessile flowers borne in terminal, bracteate heads,
salverform (funnelform in *L. serrulatus*) corollas with filiform tubes
much exserted beyond the calyx of herbaceous lobes with mem-

TABLE 1. COMPARISON OF SELECTED CHARACTERS OF *LINANTHUS LATISECTUS* AND RELATED SPECIES. Measurements in mm were made on fresh specimens. n = sample size. SE = standard error.

Characters	Species		
	L. latisectus (n = 137)	*L. androsaceus* (n = 132)	*L. parviflorus* (n = 214)
Leaf/stem angle	ca. 90°	<90°	<90°
Degree of calyx glandularity	high	none	medium (rarely none)
Middle leaf lobe width (mm)	mean = 2.5 (SE = 0.04)	mean = 1.6 (SE = 0.03)	mean = 1.4 (SE = 0.02)
Undivided portion of leaf blade length (mm)	mean = 3.5 (SE = 0.10)	mean = 2.8 (SE = 0.10)	mean = 2.6 (SE = 0.04)
Corolla limb diameter (mm)	mean = 15.5 (SE = 0.10)	mean = 18.6 (SE = 0.10)	mean = 10.7 (SE = 0.04)
Corolla tube length (mm)	mean = 22.4 (SE = 0.30)	mean = 16.8 (SE = 0.20)	mean = 29.5 (SE = 0.30)
Corolla lobe shape	broadly oval to obovate	elliptic to oval	elliptic to narrowly oval

branes between the lobes. The *L. androsaceus* complex is characterized by possession of an inconspicuous membrane between the calyx lobes below the sinuses. *Linanthus latisectus* clearly belongs in sect. *Leptosiphon* as evidenced by its floral features and to the *L. androsaceus* complex based on its calyx morphology. Within the species complex, it is morphologically most similar to *L. androsaceus* and *L. parviflorus* (Buxton 1993). Mason (1948) suggested that *L. androsaceus* is polymorphic; an affinity between between *L. androsaceus* and *L. parviflorus* has been widely accepted since he reduced the latter to a synonym of several subspecies of *L. androsaceus* (Mason 1951). Unfortunately, Mason's treatments are ambiguous and not always supported by specimens. Danforth (1945), Thomas (1961), Howell (1970), Hoover (1970), Patterson (1993), and Buxton, providing evidence based on a morphometric study (Buxton 1993), contend that *L. parviflorus* is a distinct species as described by Bentham (1833).

Vegetatively, *L. latisectus* differs from *L. androsaceus* and *L. parviflorus* in several characters, including orbicular cotyledons, an inflorescence with few bracts, and a densely glandular-pubescent calyx with long, soft marginal trichomes. It is most clearly differentiated by its leaves. The undivided portion of the leaf blade is positioned at a 90° angle to the stem; the 3–5(7) oblong to spatulate, recurved divisions are commonly rounded at the apex. Floral features distinguishing *L. latisectus* from the other taxa include corolla limb diameter and tube length, which are intermediate between those of *L. androsaceus* and *L. parviflorus,* its broadly oval to obovate corolla

lobes, and its glabrous to very sparsely puberulent corolla tube. Salient morphological differences among the three species are summarized in Table 1.

Furthermore, in contrast to *L. androsaceus* and *L. parviflorus,* the corolla in *L. latisectus* rarely closes after initial anthesis, thus remaining open on cloudy, cold, or rainy days, and throughout the night until senescence. This may have implications concerning comparative reproductive biology of these three species and of all the species within the *L. androsaceus complex.*

Linanthus latisectus is sufficiently distinct to merit specific rank; not recognizing it as such obscures the taxonomic relationships in the *L. androsaceus* complex in general, and among the three taxa discussed in particular. *Linanthus latisectus* does not key in major floristic manuals (Abrams 1951; Munz and Keck 1959; Hickman 1993). It is, nevertheless, abundantly represented in herbaria in western North America, most commonly referred to *L. androsaceus* ssp. *androsaceus* or to *L. a.* ssp. *luteus* (Benth.) H. Mason, although few of the character states delimiting those species (Bentham 1833; Mason 1951) are characteristic of *L. latisectus.* The following key separates those species in sect. *Leptosiphon* whose distributional ranges overlap with that of *L. latisectus.*

1. Calyx membrane wider than herbaceous lobes ....*L. ciliatus*
1'. Calyx membrane inconspicuous
    2. Calyx non–glandular
        3. Corolla limb diameter 16–22 mm ....*L. androsaceus*
        3'. Corolla limb diameter 8–11 mm ....*L. bicolor*
    2'. Calyx glandular, or if non–glandular then corolla tube 22–45 mm long (*L. parviflorus*)
        4. Corolla limb diameter 14–18 mm; middle lobes of upper leaves 2–3.5 mm wide ....*L. latisectus*
        4'. Corolla limb diameter < 14 mm; middle lobes of upper leaves < 2 mm wide
            5. Corolla tube 22–45 mm long ....*L. parviflorus*
            5'. Corolla tube 8–16 mm long .... *L. acicularis*

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DAMAGE AND RECOVERY IN SOUTHERN SIERRA NEVADA FOOTHILL OAK WOODLAND AFTER A SEVERE GROUND FIRE

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ABSTRACT

Mortality, epicormic sprouting, basal sprouting, and fire scar formation were evaluated in 148 tagged oak trees in a blue oak woodland in Sequoia National Park, California, for two years after a severe ground fire. Fire-caused mortality was low, 6% in *Quercus douglasii* and 11% in *Quercus wislizenii*. Epicormic sprouts developed in 65% of *Q. douglasii* and were most frequent in trees with more than 50% of the crown scorched. *Quercus wislizenii* showed less epicormic sprouting but developed basal sprouts more frequently. New fire scars developed on a majority of the *Q. douglasii* trees, even in areas of low fire intensity. Despite the severity of the fire, *Q. douglasii* crown recovery was almost complete within two years of the fire. *Quercus wislizenii* was reduced in importance on the site but will regain in canopy cover as basal sprouts develop from shrub form into trees.

The dominant oak of the foothill region of the Sierra Nevada, California, *Quercus douglasii* Hook. & Arn. (blue oak) is a focus of concern because of an apparent lack of regeneration (Muick and Bartolome 1987; Lang 1988) and the conversion of land for urban uses. Recent studies have indicated that fire played a significant historical role in the structure and maintenance of blue oak woodlands (McClaran and Bartolome 1989; Mensing 1991). Fire may have maintained blue oak savannas before European settlement in the mid–1800's; however, during the past century of fire suppression, ingrowth of pine and live oak has created a highly flammable condition (Griffin 1977; Parsons 1981). Information on the effects of fire is limited for the extant oak woodland (Barbour 1988), although relationships between damage and postfire survival in conifers have been well studied (Peterson and Arbaugh 1986; Ryan and Reinhardt 1988).

Low-intensity fires usually cause non-lethal damage to mature California oak trees; however, high-intensity fires can cause severe damage and high levels of mortality (Plumb 1980). Response to
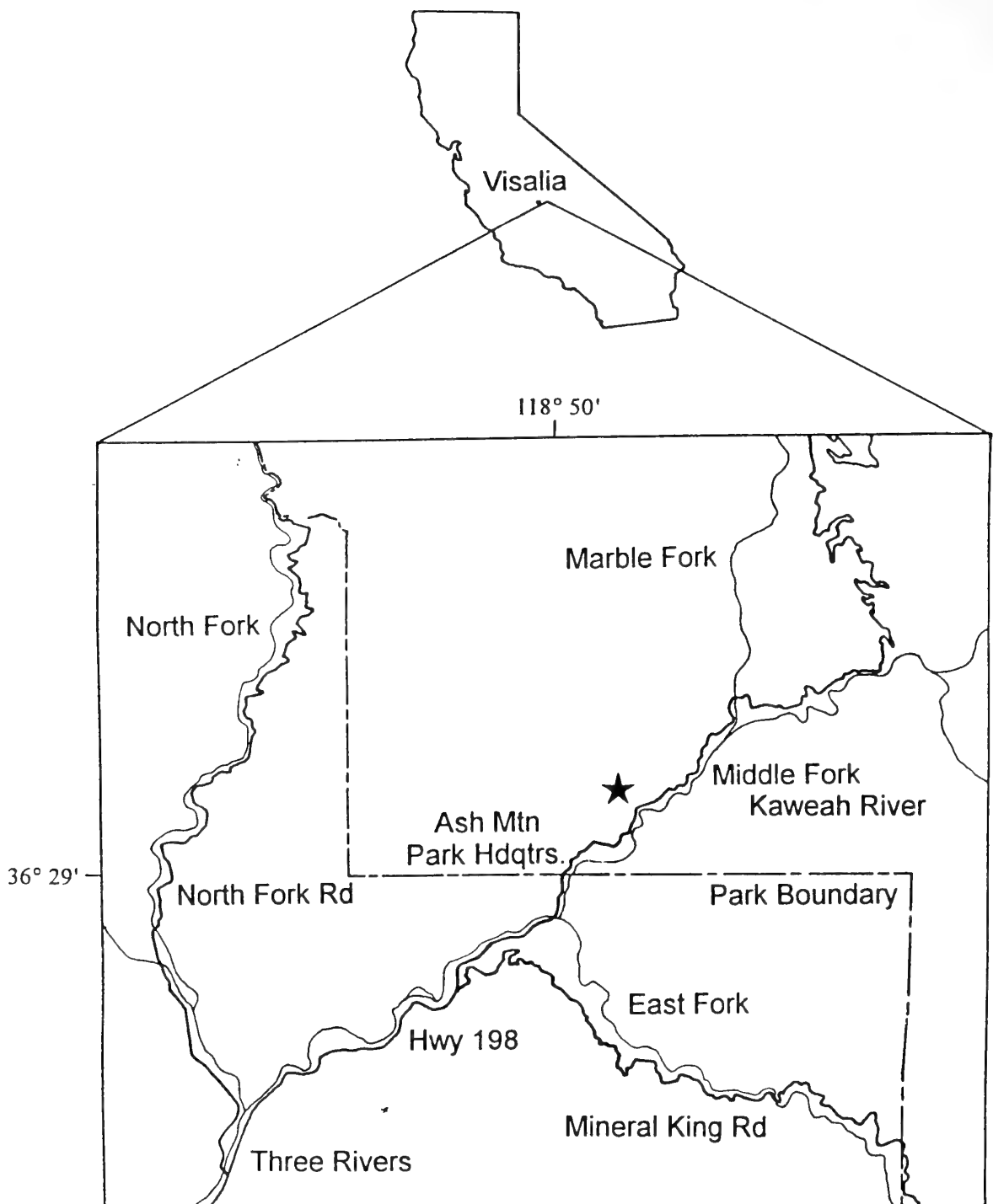
Fig. 1. Location of the study area in the southwest Sierra Nevada, California.

burning varies greatly among species. In California evergreen species, *Quercus agrifolia* Nee (coast live oak) recovers quickly while *Quercus wislizenii* A.DC. (interior live oak) is very susceptible to death of the bole (Plumb and Gomez 1983). Ground fires can cause different responses than crown fire. In a study conducted one year after an extensive 1977 fire, *Quercus lobata* Nee (valley oak) were severely damaged by intense crown burning (48% mortality) but had a relatively high degree of recovery (18% mortality) in areas of severe ground fire (Griffin 1980).

The most important postfire survival mechanism in many oaks is sprouting from dormant buds in the tree crown or on the bole (epicormic sprouting) or in the root-collar zone (basal sprouting) (Plumb and McDonald 1981). Survival also correlates with bark characteristics such as outer and inner bark thickness and surface texture, with thick bark conferring greater protection to the cambium (Plumb and Gomez 1983). Fire scars cause long–term damage to oaks, predisposing the tree to rot and failure (Plumb 1980). Dating of scars has allowed reconstruction of fire histories (McClaran and Bartolome 1989; Mensing 1991), despite the assumption that most grass or woodland fires do not result in a sufficient scar record (Parsons 1981).

Variation in fire sensitivity between two common oak species in the sierran phase of the blue oak woodland (Barbour 1988), *Q. douglasii,* a deciduous species, and *Q. wislizenii,* an evergreen, may affect stand structure and composition for decades after a fire. Mortality, crown damage, basal sprouting, and scar formation were studied in blue oak woodland after a severe ground fire that occurred in June 1987. This paper reports on the results of a two-year postfire evaluation to assess the recovery of the woodland in the absence of mitigation through management, such as culling burned trees or reseeding.

STUDY SITE AND METHODS

The study site is located in the foothill region (elevation 579 m) of the Kaweah River drainage, Sequoia National Park, Tulare County, California, in the southwestern portion of the Sierra Nevada (Fig. 1). Mean annual precipitation is 66.5 cm, although the range was 40 to 50 cm during the period of the study (25 to 40% below average). The soils are classified as thermic–Ultic Haploxerolls derived from a complex of granitic and metamorphic parent material and are coarse, well drained, and low in organic matter (Huntington and Akeson 1987).

The site spans a steep southeast-facing hillside of open blue oak/ live oak savanna with an understory of annual grasses, predominantly *Avena fatua* L. (wild oats) and *Bromus hordeaceus* L., and *Centaurea melitensis* L. (star thistle), grading into a more mesic mixed woodland of blue oak, interior live oak, and *Aesculus californica* (Spach) Nutt. (California buckeye) in a west-facing draw. The Blue oak-interior live oak/grass (QUDO-QUWI/GR) subseries of the blue oak community classification (Allen-Diaz and Holzman 1991) describes the vegetation sufficiently well, with the exception that *Pinus sabiniana* Douglas (foothill pine) is absent from the Kaweah drainage. Basal area of *Q. douglasii* (12.5 m²/ha) on the site is greater than the mean (5 m²/ha) of the QUDO-QUWI/GR subseries, although total density of the stand is somewhat lower (155 trees/ha) than the series (198 trees/ha). Very few seedlings or saplings

are present. The diameters of the trees range from 6 to 75 cm at 1.37 m (dbh). Shrub density is very low (39 stems/ha).

There has been little human use of the site since the designation of Sequoia National Park in 1890. Grazing and frequent burning occurred in the Kaweah drainage from 1869 to 1890 during the period when the foothills were explored and settled (Vankat and Major 1978). Earlier, a substantial indigenous population inhabited the area. However, their numbers declined rapidly following the arrival of Europeans (Dilsaver and Tweed 1990). Park records dating from 1925 did not report any known burns on this site. Moderate grazing by National Park Service pack stock last occurred in 1977. Grazing was not allowed during the two years of this study.

The arson-caused fired was ignited during the night of June 26, 1987, about 400 m north of the Ash Mountain park headquarters along the General's Highway. Initial fire conditions were extreme, with air temperatures in the range of 30°C, relative humidity of 17%, and fine fuel moisture of 3.5%. The fire burned on slopes of 20° to 39°. Dry grass was the primary carrier of the fire. Flame lengths were estimated at 1 to 4.6 m. Cooler down-canyon breezes began after midnight and raised relative humidity to about 50%, considerably moderating the fire's intensity.

The extent of crown damage suggested that the fire burned most of the site as a "severe ground fire" in the sense of Griffin (1980) in which trees still had leaves but the leaves were dead. The remainder burned as a "moderate ground fire" in which the upper crowns remained green, except in the mesic area of the draw where the fire backed downhill and crowns were only slightly scorched. Observations made of weather and fuel conditions during the fire were used to develop estimates of fireline intensity, a measure of the rate of energy release at the flaming front (Rothermal 1983). Fireline intensity at the fire front ranged from 315 to 1072 kW/m, while backing fireline intensity may have been as low as 17 kW/m.

The study was established in the autumn following the burn (1987). To capture the variation in fire intensity, I stratified the burn to- pographically into four transects: northwest (WEST), ridge (RIDGE), lower southeast slope (EAST1), and upper southeast slope (EAST2). The RIDGE, EAST1, AND EAST2 transects were burned by head- ing and flanking movement of the fire, while the WEST transect burned under flanking and backing conditions. The RIDGE transect experienced the highest fire intensity. Although it was not the steep- est area of the burn, it was above the location where the arsonist started the fire.

Along each 300 m transect, trees were selected for long-term eval- uation using the point-centered quarter method at 30-meter sam- pling intervals (Mueller-Dombois and Ellenberg 1974). In each of four quarters, the closest tree to the sampling point was tagged and height and diameter at breast height measured. The tree was in-

spected for fire damage including visual estimation of percent of crown scorched, height of crown scorch (measured with a clinometer), degree of basal char on the tree bole, presence of scars, and evidence of sprouting from epicormic of basal buds. If the closest tree in a quarter was dead, the dead tree was tagged and the next closest live tree was selected also. Scorched leaves did not abscise, thus it was possible to determine the extent of crown scorch in the autumn after the fire. Of the 164 tagged trees, 148 were oaks.

Each tagged tree was reassessed twice, at one-year intervals, to determine survival, sprouting, crown recovery, and fire scar development. I distinguished between aboveground mortality (topkill) in which the root system remained viable after death of the stem and regenerated a new stem or stems, and complete mortality, in which the root and aboveground stem were dead. Additional data on tree and shrub species composition, tree diameter, survival and resprouting were collected from fixed-area 0.05 ha circular plots centered around the sampling points eighteen months after the fire. A survey for seedlings and saplings (<1.37 m) was conducted in forty two 0.05 ha circular plots along the transects after the second postfire growing season. Acorn production was assessed in early autumn 1988, using Graves' (1980) rating scale; however, acorn production was negligible during the period of the study and the data will not be reported further.

One-way analyses-of-variance (ANOVA), and Scheffe means tests were used to test for significant differences in fire damage characteristics between transects and between size classes of tagged trees. This wildfire was an event without possibility of replication, so observations of fire damage on trees were not independent and did not fully meet the assumptions of ANOVA. Tests of significance were conducted at the $\alpha = 0.05$ level, however, the P-values for ANOVA results may be less than stated. Chi square tests were used to assess significance of the binomial variables of mortality, sprouting, and fire scar development. Binary logistic regression was used to investigate the relationship of mortality and resprouting responses with tree and fire damage characteristics. Logistic regression has been used to identify important variables or to develop predictive models in situations where the outcome is restricted to one of two populations, such as tree mortality from fire (Ryan and Reinhardt 1988) or resprouting after fire (Davis et al. 1989). Variables tested in the logistic regression models included site characteristics, such as slope and topographic location, and individual tree attributes such as diameter and the presence of scars.

RESULTS

Fire intensity. Fire damage characteristics, percent of crown scorched, scorch height, and bole char height, all differed significantly

TABLE 1. SITE CHARACTERISTICS, FIRE DAMAGE AND FIRE EFFECTS (TWO YEARS POSTFIRE) ON TAGGED OAK TREES FROM FOUR TRANSECTS IN THE ASH MOUNTAIN FIRE. Within rows, means with different letters indicate significant differences at P < 0.05 by ANOVA. Significant chi-square results are indicated with **.

	Transect			
	WEST	RIDGE	EAST1	EAST2
Site characteristics				
Aspect	283°	149°	92°	108°
Slope percent	67	30	70	52
Canopy cover (%)	47	31	30	30
Oak trees per transect (n)	31	38	37	42
Fire damage				
Mean crown scorch (%)	27 a	90 b	45 ac	54 c
100% crown scorch (n)	3	28	9	6
Mean scorch height (cm)	36 a	58 b	50 ab	50 ab
Mean bole char height (cm)	20 a	60 ab	50 a	100 b
Fire Effects				
Above ground mortality (%)	0	19	5	9
Basal sprouting (%)**	7	32	8	24
Fire scars (%)	65	59	64	40

between transects when analyzed by one-way ANOVA (Table 1). Crown scorch was significantly higher on RIDGE transect where 82% of all trees had completely scorched crowns. All fire damage characteristics of the WEST transect were less severe than those of the other transects. Despite the differences between these indicators of fire severity, chi square tests found no significant differences in mortality between transects, however, there were highly significant differences in the degree of basal sprouting. Basal sprouting on the mildly burned WEST transect was lower than expected, while the hotly burned RIDGE plot had more basal sprouting than expected.

Mortality. Immediate mortality of oak trees due to the fire was low; only two of 148 tagged oaks died during the fire. One *Q. douglasii* tree had extensive damage from previous fire scars and collapsed while burning, and one *Q. wislizenii* of very small diameter was severely burned and did not resprout.

By two years after the fire, aboveground mortality of tagged trees was much higher for *Q. wislizenii* (24%) than *Q. douglasii* (8%). Complete death of the individual occurred in 6% of *Q. douglasii* trees and in 11% of *Q. wislizenii* trees (Fig. 2). All *Q douglasii* trees whose main stems died produced epicormic sprouts, basal sprouts or both before dying, however, only two still had surviving basal sprouts in 1989. By contrast, more than half of topkilled *Q. wislizenii* trees had surviving basal sprouts two years after the fire. Death or
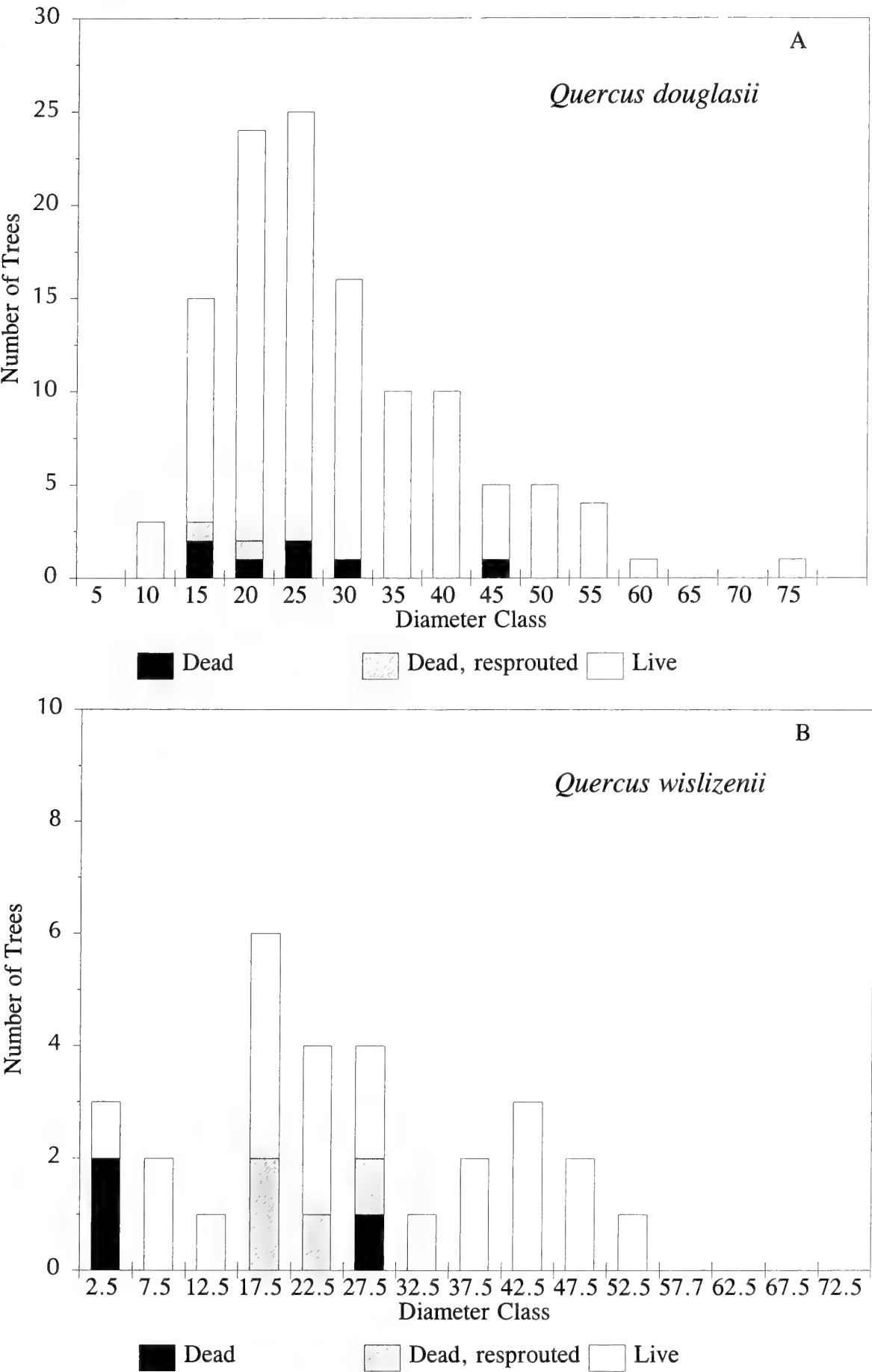
FIG. 2. Mortality of tagged *Q. douglasii* (A) and *Q. wislizenii* (B) by size class two years postfire. The category "Dead, resprouted" indicates dead boles with basal sprouts surviving two years after the fire.

TABLE 2.   NUMBERS AND MORTALITY RATE OF *Q. DOUGLASII* AND *Q. WISLIZENII* AS
RELATED TO DEGREE OF CROWN SCORCH DURING TWO YEARS OF POSTFIRE EVALUA-
TION.

| Species: | Percent of crown scorched | | | | | | | |
| | *Q. douglasii* | | | | *Q. wislizenii* | | | |
Year	≤25	26–50	51–75	100	≤25	26–50	51–75	100
1987	39	20	22	36	9	7	7	8
1988	39	19	22	36	9	7	7	2
1989	39	19	21	30	9	7	4	2
Mortality	0%	5%	4.5%	16.7%	0%	0%	43%	75%

physical failure of large stems in multiple stem *Q. wislizenii* trees
was common but did not lead to death of the whole tree.

The small numbers of both species that died limited statistical
analysis. Percent of crown scorched and the presence of old fire scars
were the only factors which predicted the probability of mortality
in logistic regression models. Mortality was greatest in trees with
100% of the crown scorched, both marked differences between spe-
cies were found (Table 2). Seventeen percent of *Q. douglasii* trees

■ *Q.douglasii*   ▨ *Q.wislizenii*
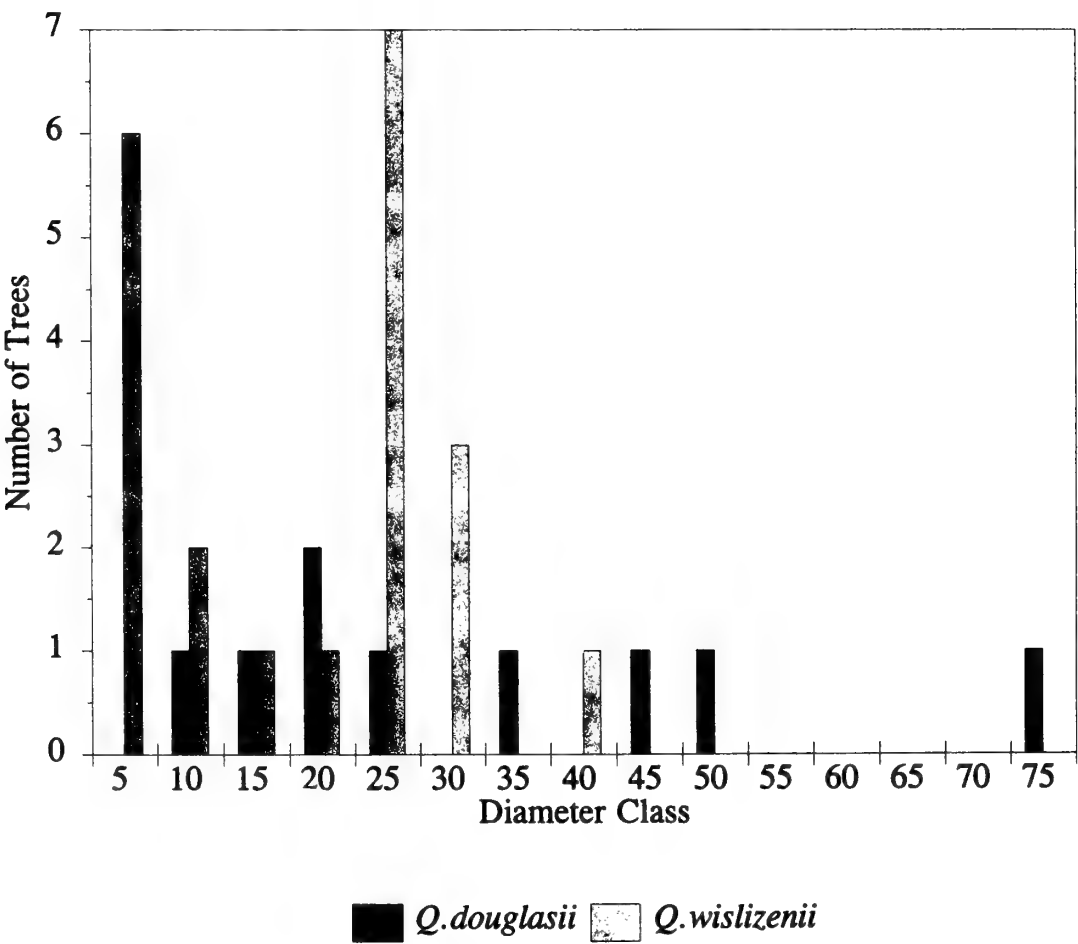
FIG. 3.   Aboveground mortality, by diameter class, of oak trees sampled in fixed
area plots eighteen months after the fire.

TABLE 3. STAND CHARACTERISTICS OF THE ASH MOUNTAIN FIRE SITE EIGHTEEN MONTHS AFTER THE JUNE 1987 FIRE.

Species	Density (stems/ha)		Basal Area (m²/ha)	
	Live	Dead	Live	Dead
Trees				
Aesculus californica	18	0	2.5	0
Fraxinus dipetala	11	9	0.2	0.1
Quercus douglasii	109	5	12.5	0.5
Quercus wislizenii	17	13	4.5	0.1
Shrubs				
Arctostaphylos viscida	5	3		
Cercocarpus betuloides	3	3		
Rhamnus crocea	5	0		
Toxicodendron diversilobum	15	0		
Yucca whipplei	5	0		

with complete crown scorch died within two years, whereas 75% of *Q. wislizenii* trees with that degree of crown scorched died.

Data collected in the fixed-area plot survey eighteen months after the fire indicate that 45% of *Q. wislizenii* trees in this sample experienced aboveground mortality and only one of 46 *Q. wislizenii* individuals had died. The average diameter of topkilled *Q. wislizenii* was 18 cm and was significantly smaller than the diameter of the surviving boles of this species. Of the 163 *Q. douglasii* trees sampled in these plots, the aboveground mortality rate was 5% and the true mortality was 4%. Aboveground mortality in this species was not related to diameter size class (Fig. 3). Basal area of dead trees was very low, less than 4% of the total basal area for each oak species (Table 3).

Crown damage and recovery. Epicormic sprouts developed in almost twice as many *Q. douglasii* trees as *Q. wislizenii*. Within two weeks after the fire, large, bright green epicormic leaves were observed in the crowns of heavily scorched *Q. douglasii* trees. By six months after the fire, 65% of all *Q. douglasii* trees had epicormic sprouts developing in the crown and on the boles. Epicormic sprouting occurred most frequently in trees with more than 50% of the crown scorched (Fig. 4) and occurred in all size classes. Percent of crown scorched was the only significant factor predicting likelihood of crown sprouting identified by analysis with logistic regression. Sprouting within the crowns of *Q. wislizenii* trees occurred in 35% of tagged trees and was restricted to trees larger than 20 cm DBH. Deer browsed on available crown and basal sprouts of both species.

The canopy cover of surviving *Q. douglasii* trees was mostly restored by two years after the fire. Overstory crown recovered less in *Q. wislizenii* because of slow growth in scorched portions of the
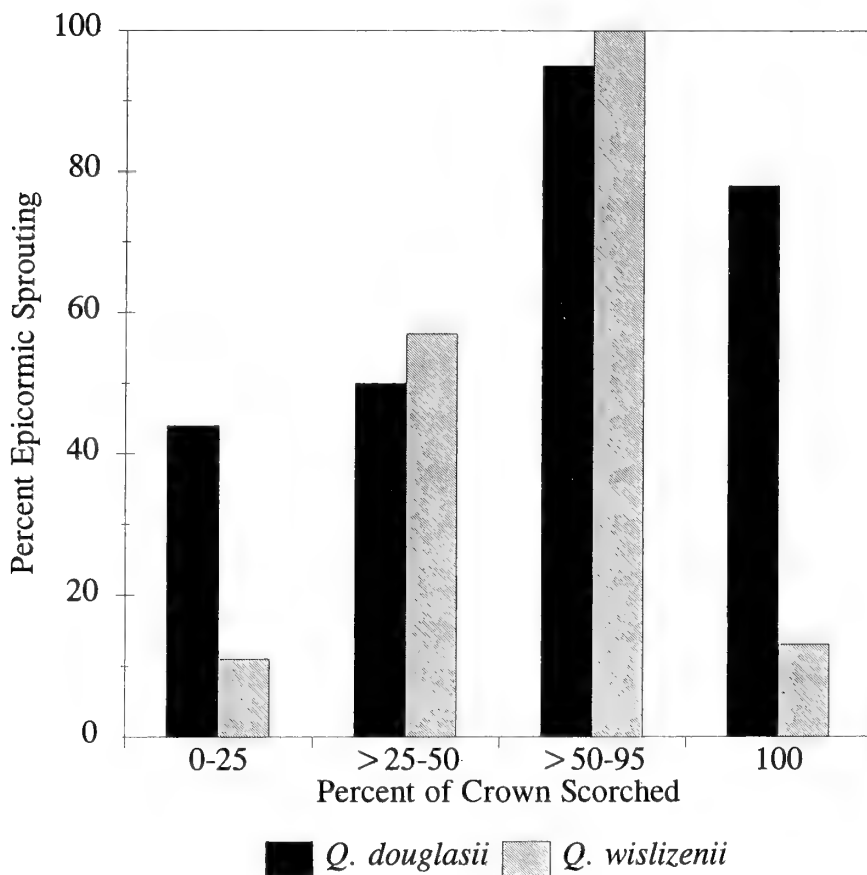
FIG. 4. Percentage of oak trees with epicormic sprouting as a function of the percent of crown scorched.

crown and the death of major stems. However, an abundance of shrubby stems growing from the root collar zone occurred in 36% of surviving *Q. wislizenii* trees. *Phoradendron villosum* (Nutt.) Nutt. (oak mistletoe) was abundant in the crowns of several trees of both species before the fire; however, once scorched, it died completely.

Scarring. Many more old fire scars were found on *Q. wislizenii* trees (86%) than on *Q. douglasii* trees (47%). New scars developed on 59% of *Q. douglasii*. New scars were not clearly discernible on *Q. douglasii* boles until two years after the fire. On some *Q. douglasii* trees, the charred bark surface flaked away and left the bole apparently unharmed. Rescarring of old wounds occurred, but many trees with old scars developed new scars in previously undamaged bark. Forty-one percent of new scars were subjectively categorized as small, 20% as average and 38% as large. New scars formed on 38% of the *Q. wislizenii* trees that had not died. Incidence of scarring did not differ significantly between size classes for either species. Although crown damage varied significantly between transects (Table 1), frequency of fire scar development did not.

Seedlings. A small number of oak seedlings were found after the fire, 9 *Q. wislizenii* and 5 *Q. douglasii*. Based on examination of the

stem, the 14 oak seedlings appeared to have established before the fire and had resprouted, and one had died after resprouting. The height of the resprouted seedlings ranged from 10 to 50 cm. The mesic WEST transect had more than half of the seedlings, all *Q. wislizenii*.

There was no evidence of establishment of fire-germinating shrub species in plots surveyed after the fire (Table 3). Some *Cercocarpus betuloides* Torrey & A. Gray (mountain mahogany) and many *Toxicodendron diversilobum* (Torrey & Gray) E. Greene (poison oak) resprouted after the fire.

Discussion And Conclusions

The role of fire in the ecology and conservation of blue oak woodlands requires clarification. Pertinent ecological questions include how much fire, if any, is necessary to maintain open savanna characteristics (Griffin 1977), what is its role in *Q. douglasii* recruitment (McClaran and Bartolome 1989) and in succession (Allen-Diaz and Holzman 1991). One effect of the increasing urbanization of the foothill region is a greater risk of human-caused fire and attendant efforts to reduce wildfire danger at the "wildland-urban interface," including prescribed burning. In reserves such as Sequoia National Park, efforts to simulate natural fire regimes require information on the responses of key species as well as sound fire history information (Parsons 1981).

Savanna-like characteristics were temporarily enhanced on this site by the fire. The results of this case study suggest that the 1987 fire, although severe, did not affect *Q. douglasii* dominance of the stand and resulted in no change in relative dominance between species (Table 3). Density of *Q. wislizenii* was reduced through aboveground mortality of smaller diameter trees with little change in basal area of that species. Shrub abundance, already low, decreased slightly after the fire.

Fire intensity in blue oak woodland has been considered too low to scar trees, resulting in incomplete fire history reconstructions (Parsons 1981). However, on this site, fire scar development was frequent even in areas that burned at low intensity. In contrast to previous assumptions, oak trees may record as scars even low-intensity fires at relatively high frequency, at least under the ambient conditions of high are temperatures and active growth stage that occurred during this fire. Hidden fire scars in intact *Q. douglasii* have been documented by examining cut cross sections (McClaran 1988); therefore my estimate of old scars may be lower than the actual number of scarred trees. Some of the small scars I observed would seemingly heal quickly. The greater number of old scars ev-

ident on *Q. wislizenii* trees suggests that they may heal scars more slowly than do *Q. douglasii* trees.

In common with other studies of *Q. douglasii* in this region (Brooks 1969; McClaran 1986), there are few *Q. douglasii* saplings and seedlings on the site. However, the resprouted oak seedlings found after the fire were generally vigorous. Recent studies of *Q. douglasii* (Allen-Diaz and Bartolome 1992) and *Quercus engelmannii* E. Greene Engelmann oak (Lathrop and Osborne 1991) discount fire as a limiting factor in seedling survival, because most established seedlings survived and resprouted after burning. Factors other than fire apparently are responsible for the failure of seedlings to survive to the sapling stage. A flush of *Q. douglasii* regeneration by sprouting from sapling-sized trees was not apparent following this fire, probably because of a distribution skewed towards larger (>20 cm) trees.

Prediction of fire effects is complicated by climatic and phenological interactions unique to each occurrence. The high survival of *Q. douglasii* trees observed on this fire indicates that severe crown injury may not result in the death of trees, despite the additional stress of low precipitation during the study period. Rundel (1980) states that there are suites of traits in many California oak species which allow survival in areas where fires are frequent. The ability of *Q. douglasii* to withstand both extreme drought and brief high-intensity fires may result in part from its deciduous characteristics, which allow it to facultatively add or excise leaves in relatively rapid response to environmental stress. Persistent basal sprouting in *Q. wislizenii* is one factor that allows this species to remain in the blue oak savanna environment; however, reduced survival after fire damage to crown and bole may limit its dominance in this phase of the oak woodland.

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ATRIPLEX ASTEROCARPA (CHENOPODIACEAE), A NEW SPECIES FROM SOUTHERN UTAH AND NORTHERN ARIZONA

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Abstract

Atriplex asterocarpa is a newly described annual species from southern Utah and northern Arizona. It occurs most often on slopes of the Chinle Formation. It is morphologically closest to *A. saccaria* but differs in its long-petioled leaves, globose fruiting bracts and indurate, sharp-pointed, conical fruiting-bract appendages.

A morphologically distinct, new annual species of *Atriplex* was discovered by the first author, 20 June 1973, on a south-facing slope in talus derived from the Chinle Formation near Hite Crossing, ca. 10 miles southeast of Hog Spring, T33S R13E S1, Garfield Co., Utah. Examination of all annual species of *Atriplex* in several herbaria (ASC, BRY, CAS, GH, MONT, NY, RM, RSA, UC, US, UT and UTC) showed twelve previous collections of the new species. They were each labelled *A. saccaria* S. Watson.

Atriplex asterocarpa Stutz, Chu and Sanderson, sp. nov. (Fig. 1).— Type: USA, Utah, Garfield Co., ca. 5 mi SE of Hog Spring, Highway 95, mile marker 39, T34S R13E S1, 1280 m, 23 Jul 1991, *H. C. Stutz 95575* (type, BRY).

Herbae annuae, 15–30 cm altae; caulis erectus vel ascendens, multo ramosus a basi ad apicem; rami oblique patuli, fere teres, in parte superiore dense furfuracei, in parte inferiore glaberi. Folia alterna, petiolata; laminae ovatae usque anguste-ovate, 1–2.5 cm longae, 0.5–1.5 cm latae, apice acutae, basi cuneatae, integeri, utrinque dense furfuracea; petioli 2–12 mm longi. Planta monoecia; staminales flores brevissimis pedicellis; glomerati, in terminales spicas 1–3 cm longos; perianthium fere globosum, circa 1.2 mm in diam.,
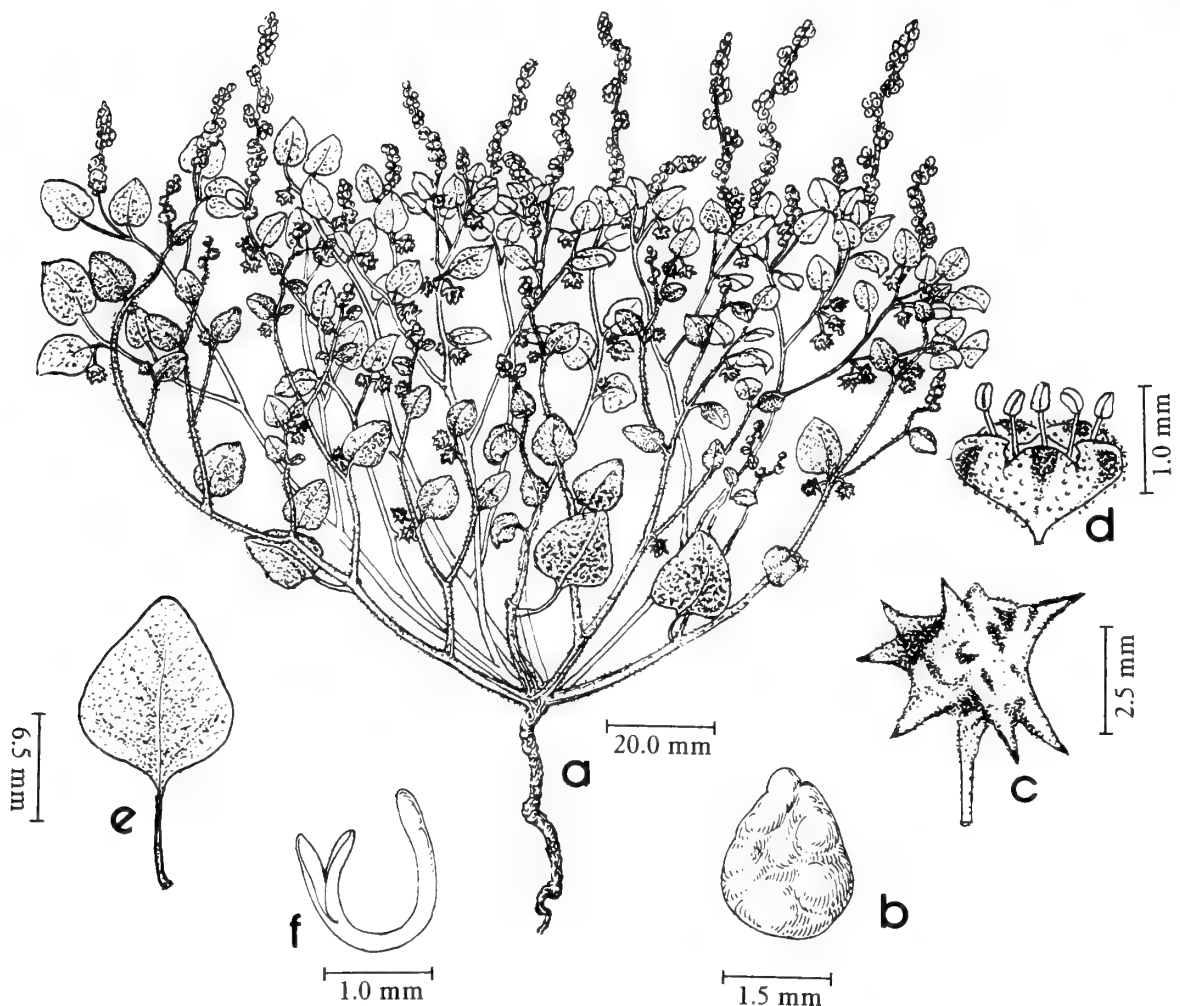
Fig. 1. *Atriplex asterocarpa*. a. Habit. b. Seed. c. Fruiting bract. d. Male flower. e. Leaf. f. Embryo. (Drawings by Xia Quan.)

5-partitum, segmentis oblongo-ovatis, membranaceis, circa 0.9 mm longis, extus furfuraceis; stamina 5, antheris circa 0.4 mm longis et filamentis segmentis leviter brevioribus; pistillati flores glomerati in fere omnium foliorum axillis sub staminatibus inflorescentiis, bracteolis connatis ad vertices, stigmis 0.4–1.2 mm longis et style inconspicuo; fructiferi bracteae globosae, 5–6 mm in diam., saepe cum stipite 2–4 mm longi, perfecte obducti appendicibus conoideis, induratis, apice pungentibus. Utriculus ovatus; semen circa 2.5 mm longum, testa membranacea, rubri-brunneola et radicula supera. Chromosomatum numerus $2n=18$. Proxima *A. saccariae* S. Wats. et *A. cornutae* Jones, illa differt foliis cordatis et sessilibus, haec differt appendicibus molliter columnaribus.

Annual herb, 15–30 cm tall. Stems erect, with crowded branches from base to top, the branches oblique-spreading or decumbent, nearly terete, basal part glabrous, terminal part densely scurfy. Leaves alternate, mostly long-petioled; blades ovate to narrow-ovate, 1–2.5 cm long, 0.5–1.5 cm wide, acute at apex, cuneate at base, entire,

densely scurfy on both surfaces, venation kranz-type; petiole 2–10 mm long. Plants monoecious; staminate flowers with short pedicels, glomerules in spikes 1–3 cm long at end of branches; perianth nearly globose, ca. 1.2 mm in diam., 5-parted, segments oblong-ovate, membranaceous, ca. 0.9 mm long, scurfy abaxially; stamens 5, anthers ca. 0.4 mm long, filaments slightly shorter than perianth segments. Pistillate glomerules in axils of most leaves; bracteoles fused to summit; stigma 0.4–1.2 mm long, style inconspicuous; fruiting bracts globose, 5–6 mm in diam., with several cone-shaped, indurate, sharp-pointed appendages on both surfaces, scurfy, usually with a stipe 2–4 mm long. Utricle ovate; seed ca. 2.5 mm long, tests membranaceous, red-brown, radicle superior. Chromosome number: $2n=18$.

PARATYPES: USA, Utah, Garfield Co.: top of Entrada Standstone, ca. 4 miles N of Utah Hwy 96 junction with Burr Trail Road, 3 Sep 1970, *S. L. Welsh 10898* (NY, BRY); ca. 5 mi SE of Hog Spring, Hwy 95, T34S R13E S1, 20 Jun 1973, *H. C. Stutz 7247* (NY, BRY); 1.9 miles NW of Hite Crossing, Highway 95, 20 Jun 1973, *H. C. Stutz 7279* (BRY); due NW of Bullfrog on Shitamaring Road, 4500 ft elevation, 29 Jun 1977, *E. Neese and S. White 3446* (BRY); Talus slopes, about 10 mile S of Hite, 130 miles N of Glen Canyon dam site, Colorado River, 22 Jun 1973, *H. C. Stutz 7255* (NY, BRY, UT); Bullfrog creek crossing on Notom Road, 3750 ft elevation, 18 Jun 1977, *E. Neese and S. White 3438* (NY, BRY); ca. 3 miles NW of Hite Crossing, Hwy 95, mile 39, west-facing slopes, 5 Jun 1992, *H. C. Stutz 95634* (BRY); Bullfrog Marina, 2 miles W of Hwy 276 on Nodom Road, 21 May 1993, *H. C. Stutz 95807*. San Juan Co.: Junction of Nokai Creek and San Juan River, 19 miles NW of Oljeto Post, 18 Jun 1938, *H. C. Cutler 2276* (UC, GH, MO, US); Piute Canyon, ca. 6 miles E of Navajo Mt. 24 Jun 1973, *N. D. Atwood and Trotter 5353* (BRY); White Canyon, salt desert, 1250 m elevation, 10 Aug 1983, *L. C. Higgins 14183* (NY, BRY); Clay Hills Divide, ca. 2130 ft elevation, 23 May 1983, *L. C. Higgins and S. Welsh 13229* (NY, BRY); White Canyon, Lake Powell, 3800 ft elevation, Chinle form. Shadscale comm. 13 May 1983, *S. L. Welsh 22015* (NY, BRY, RM); NE ¼ S25 T35S R13E, lower SW flank of mesa ca. 1 mile, ca. 3950 ft elevation, dissected slopes/badlands of Chinle Formation, 3 May 1987, *J. S. Tuhy and J. S. Holland 3090* (UT); Blue Notch, ½ mi west of Summit, T35S R13# J36, 8 Apr 1993, *H. C. Stutz 95761*. Arizona, Coconino Co., vic. Vermillon Lodge, steep rocky south slope, 4200 ft elevation, 18 Apr 1978, *R. K. Gierish 4194* (ASC); Lee's Ferry, south-facing slope, Chinle Formation, 23 May 1993, *H. C. Stutz 95792* (BRY).

Taxonomic relationships. Atriplex asterocarpa superficially resembles *A. saccaria* Wats. and *A. cornuta* Jones, but is easily distin-
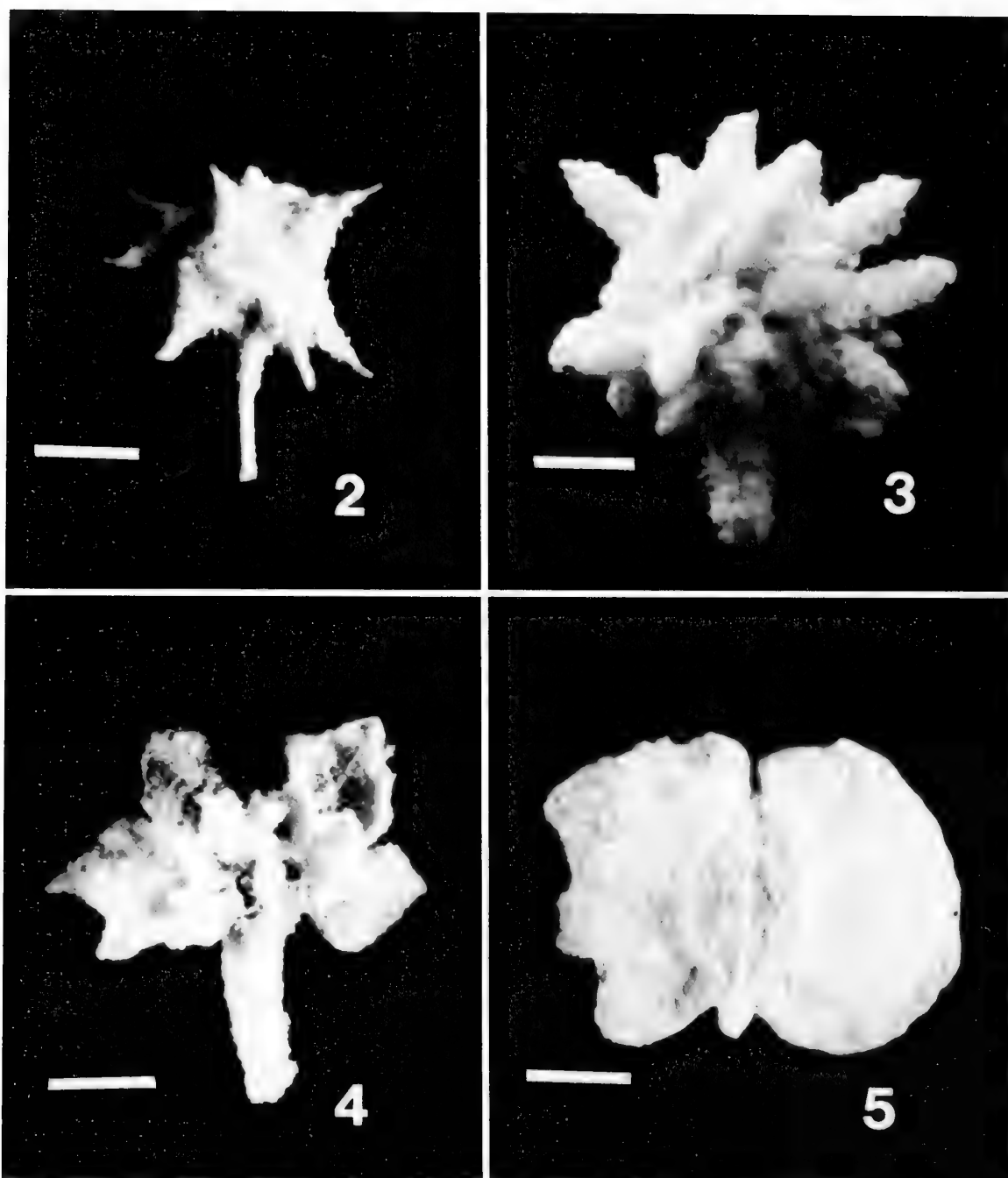
FIGS. 2–5. Fruiting bracts of the four *Atriplex* species in Series *Saccariae* (scale bars = 2 mm). 2. *A. asterocarpa.* 3. *A. cornuta.* 4. *A. saccaria.* 5. *A. graciliflora.*

guished from them by its long-petioled leaves and its long-pedicelled, globose fruits that are profusely covered with indurate, conical, sharp-pointed appendages (Fig. 2). Also, *A. asterocarpa* never produces small, cuneate, truncate, smooth-surfaced fruits as found, usually in few numbers, on most plants of *A. saccaria* and *A. cornuta.*

Atriplex asterocarpa also superficially resembles *A. graciliflora* Jones but *A. graciliflora* is easily distinguished by the pair of broad wings produced on its fruiting bracts (Fig. 2).

Atriplex asterocarpa, A. saccaria, A. cornuta and *A. graciliflora* appear to form a natural distinguishable group (Series *Saccariae*),

collectively distinct from other species of *Atriplex* in several features including the formation of a double layer of persistent, vesicular, usually stalked, trichomes on their foliage and fruits. During the life of the plant and even after drying, these spherical trichomes remain intact, thereby resulting in a sandpaper appearance to the vegetative surfaces. In contrast, trichomes of other *Atriplex* species break open soon after forming, resulting in vegetative surfaces having a flat, glistening, furfuraceous appearance. Also *A. asterocarpa, A. cornuta, A. Graciliflora,* and *A. saccaria* are all endemic to the Colorado Plateau of Utah, Arizona, New Mexico and Colorado and unlike most other annual *Atriplex* species, grow primarily on badland clay soils, often in monocultures, or with only a few other associated species. All four species are consistently diploid with $2n=18$ chromosomes (determined from aceto-carmine squashes of pollen-mother-cells derived from anthers of staminate flowers fixed in 5% acetic acid and stored in 70% ethyl alcohol).

Distribution and habitat. Atriplex asterocarpa is sporadically abundant in southeastern Utah and northern Arizona. It is mostly restricted to soils derived from the Chinle Formation, but some populations north of Lake Powell, Garfield County, Utah, occur on Entrada sandstone. At Hite Crossing it is abundant on two large talus slumps derived from the higher up Chinle Formation but is absent from adjacent Moenkopi soils. Northwest of Hites Crossing in North Canyon, along Highway 95, dense populations occur wherever the Chinle Formation is exposed; particularly large populations, each covering 2–3 acres, occur on southwest-facing slopes above mile markers 37 and 40. At Blue Notch, ca. 25 miles southeast of Hites Crossing, there is a dense population of *A. asterocarpa* (ca. 6 plants per ft^2) occupying approximately 2 acres, on the southwest-facing slope ¼ mile below the summit. Near Lee's Ferry, Coconino County, Arizona, there are several populations on the Chinle Formation, north of the Marino, ½–3 acres in size, with densities of about 4 plants per ft^2.

Associated species. Atriplex asterocarpa often grows as a monoculture with no other attending plant species but in some populations the following species are sporadically present: *Atriplex confertifolia* (Torr. & Frem.) Wats., *Atriplex garrettii* Rydb., *Atriplex navajoensis* Hanson, *Bromus rubens* L., *Ephedra viridis* Cov., *Eriogonum inflatum* T. & G., *Stanleya pinnata* (Pursh) Britt.

Phenology. Flowering and fruiting is mostly in April and May but with late May and June rains, new seedlings may appear that flower into June and July.

During the summer and fall of 1989 and 1990 repeated searches revealed no plants of the new species in areas that were known to

have been heavily populated by them in previous years. However, during the summers of 1991, 1992 and 1993 these same areas were again occupied by dense populations, indicating that *A. asterocarpa* seeds can remain dormant and viable in seed banks for at least three years.

Seedlings derived from seeds, and seedlings transplanted from native populations, when grown in the greenhouse and nursery at Brigham Young University, Provo, UT, maintained all of the characteristics of plants growing in nature.

Key to *Atriplex* Species in Series *Saccariae*

1. Fruiting bracts with broad marginal wings, unappendaged ......*A. graciliflora.*
1'. Fruiting bracts without marginal wings, bracts appendaged.
    2. Fruiting bracts covered with conical appendages, leaves cuneate at base, distinctly petiolate.
        3. Appendages indurate, sharp-pointed ....*A. asterocarpa*
        3'. Appendages flexible ....*A. cornuta*
    2'. Fruiting bracts with flattened appendages, leaves sessile or subsessile, cordate or subcordate ....*A. saccaria*

CLASSIFICATION AND ORDINATION OF ALPINE PLANT COMMUNITIES, SHEEP MOUNTAIN, LEMHI COUNTY, IDAHO

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Abstract

The alpine vegetation in the immediate vicinity of Sheep Mountain, Lemhi Range, Lemhi County, Idaho, was investigated using data from field observations analyzed by the programs TWINSPAN and CANOCO (CCA). Percent cover of vegetation and environmental data were recorded for 77 plots. Eight communities were identified and described with respect to apparent habitat preferences. The most frequent communities are characterized by a) *Carex rupestris,* b) *Carex elynoides,* and c) *Calamagrostis purpurascens–Carex elynoides.* An exposure gradient showed the strongest correlation with the community distribution, but substrate, elevation, and slope were also found to be important. In general, the study area communities present a uniformly dry turf-like physiognomy, with some early snowbed and *Dryas* or *Salix* mat communities occasionally present.

In the last few decades, many alpine studies have been published, but of all the alpine areas in North America, Idaho alpine has received the least attention. Until recently, it was not common knowledge that Idaho has well-developed alpine communities, but this and other studies document its existence. Our observations are supported by numerous collections and studies of several researchers dating back to the 1800's. Thomas Nuttall may have made alpine collections in Idaho as early as 1834 (Mckelvey 1955), followed by L. F. Henderson (1890's), Hitchcock and Muhlick, and Davis (1940's and '50's) (Henderson 1992). The second author and students associated with the University of Idaho Herbarium have been collecting in and studying the east-central Idaho alpine since 1973. Brunsfeld (1981) completed an alpine flora for part of east-central Idaho based on collections from the Lost River and southern Lemhi ranges, and the southern Beaverhead Mountains. Caicco (1983) and Moseley (1985) have each completed community studies for selected sites in east-central Idaho.

From these collections and studies, as well as from field observations of the second author, Idaho alpine appears to be restricted to the mountains of central and east-central Idaho. The present research area, Sheep Mountain, is located in the southern Lemhi

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Range, about 32 km south of Leadore. The Sheep Mountain alpine is in excellent condition, and the site has been accepted as a candidate Research Natural Area by the U.S. Forest Service.

Other Idaho alpine studies (Caicco 1983; Moseley 1985) have documented all of the general categories of alpine communities typically seen in temperate alpine locations, e.g., fellfield, turf, meadow, and bog. Based on those studies, field observations by the second author, and the topographic and substrate variety of Sheep Mountain, we predicted that Sheep Mountain would also have a wide variety of alpine communities, some possibly unique. To test this prediction, we sampled the Sheep Mountain alpine vegetation with the goals of classifying the plant communities, describing their distribution with respect to measured environmental variables, and relating the results of the analysis to several regional studies.

STUDY AREA

The proposed Sheep Mountain Research Natural Area (RNA) (44°22′N, 113°16′W) (Fig. 1) is centered along the crest of the southeast trending Lemhi Range, and encompasses 3.2 km of ridgeline. Elevation of the RNA ranges from 3000 to 3312 m, includes approximately 220 ha, and, except for scattered individuals of *Pinus albicaulis* Engelm. in a few locations to 3025 m, the area is dominated by alpine vegetation. Sixty-six of the 77 plots sampled were located in the RNA; the other 11 were placed 0.8 km to the south on the north slope of Spring Mountain (Fig. 1). Timberline in both locations is composed of *Pinus albicaulis* and *Juniperis communis* L. associated with *Festuca ovina* L. var. *ingrata* Hackel ex Beal and *Artemisia tridentata* Nutt. Access is provided by primitive roads originating in Squaw Creek Canyon on the west side and Spring Mountain Canyon on the east.

Two parent materials, dolomite and quartzite (Ruppel and Lopez 1981), are exposed within alpine habitats with abrupt transitions between each parent material. Most of the soil is derived from dolomite, except for a few isolated bands where the parent material is quartzite.

Climatic data were estimated from regional weather stations (Myron Molnau, Office of State Climatologist, personal communication). Temperature information originates from Leadore, Idaho, elevation 1829 m, 32 km north, and was corrected for elevation (0.64°C/100 m). The coldest month is January with an average temperature of −16° C, while the warmest month is July at 9°C. Precipitation for the study area is assumed to be similar to Meadow Lake, 6.4 km to the north; total precipitation for the year is 853 mm; a unimodal pattern is evident, with the majority of moisture falling during the winter months, 110 mm in January alone. The summer months are
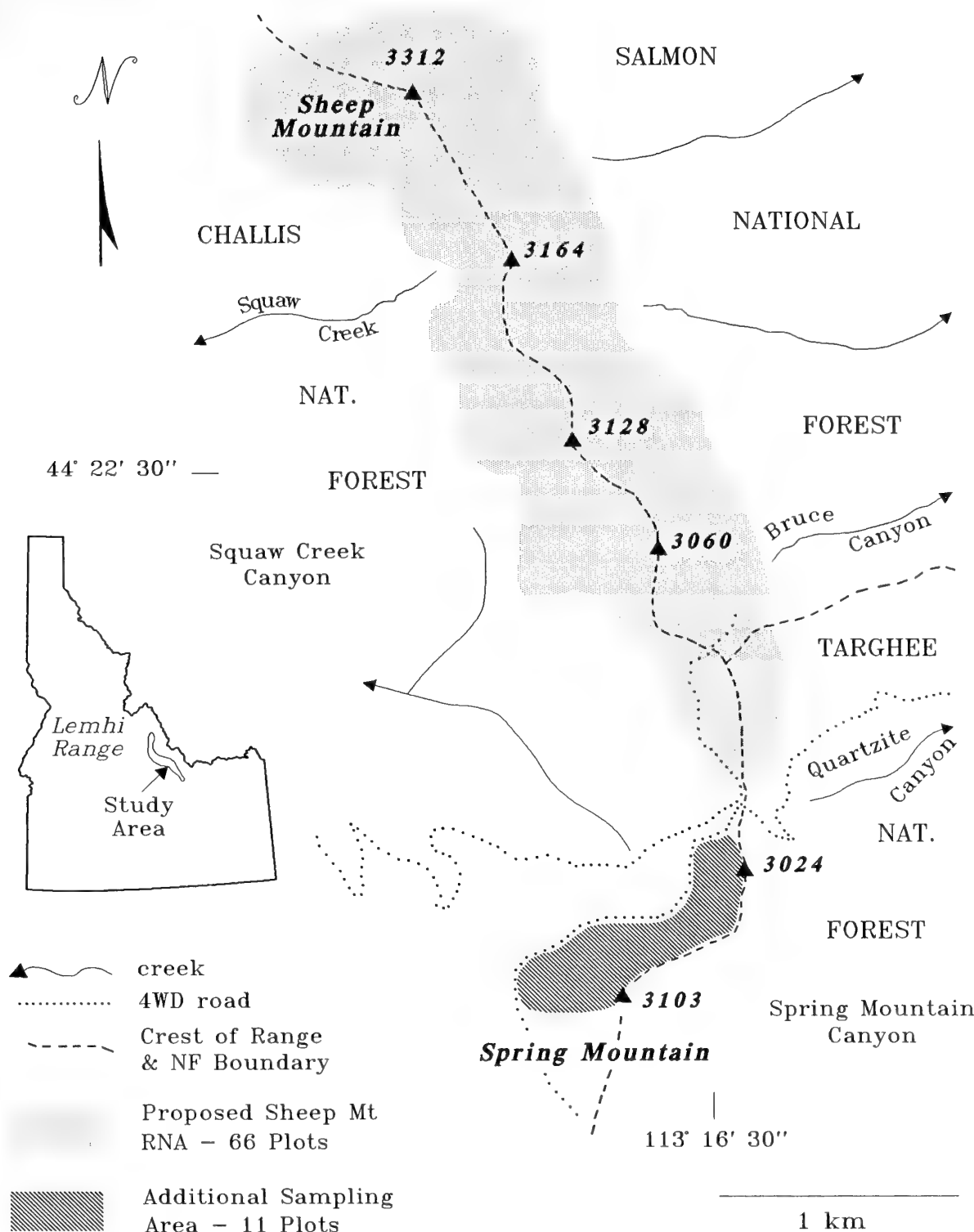
FIG. 1.   Study area location. Elevations are shown in meters.

generally dry, with only 27 mm falling in July as occasional rain-showers. Overall, the area has a mountain climate with both coastal and continental influences and prevailing winds from the west (Ross and Savage 1967) resulting in cold, wet winters, and warm, dry summers. All vegetation sampled was clear of snow by 21 June 1992 when sampling began, although lingering snowbanks were present in places.

Land use history includes mostly mining exploration, with apparently little grazing. The remains of several small mines or pits are evident, but they only insignificantly scar the area. Due to the lack of perennial moisture in the alpine, grazing has historically been insignificant; none has occurred in the past twenty years (Steve Spencer, Range Management, Lost River Range District, personal communication).

METHODS

Data collection. Fieldwork was conducted from 21 June to 25 July 1992. These dates represent the earliest opportunity to do fieldwork, to the latest, initially due to lingering snow, and then drought conditions. Only vegetation above treeline and krummholz was examined. Seventy-seven plots were sampled using the methods of Bliss (1963) and Douglas and Bliss (1977). The process begins with the identification of a homogeneous stand of alpine plants no less than 60 m² in size. All distinctively different homogeneous stands in the study area were sampled. Additionally, when size of the stand permitted, plots were arranged so as to best represent the diversity of slopes, positions on slopes, and aspects present in the stand. Within the stand a plot 4 by 8 m is measured and then further divided into eight rows, each 4 by 1 m. Replicate plots are sampled if permitted by the size of the stand. Four of the rows are randomly selected to be sampled by five quadrats, each 0.2 by 0.5 m and spaced at 0.5 m intervals. If an odd row is selected, the first quadrat is placed adjacent to the edge of the plot; whereas in an even row, the first quadrat is displaced 0.5 m. The end result is 20 quadrats with a combined area of 2 m². For each quadrat, the percent cover for all of the species was estimated visually using a quadrat constructed as described in Daubenmire (1959). The plot percent cover for a species was the average for the 20 quadrats.

Environmental data were recorded for each plot including location, elevation, slope, substrate, and exposure index. Elevation was calculated from a United States Geological Survey 7.5′ topographic map of either the Gilmore or Big Windy Peak Quadrangle. Plot substrate was identified by rock samples examined by William Rember (Department of Geology, University of Idaho). The exposure index consisted of a scale from 1 to 5, 1 being a low exposure, and reflected several environmental factors at once (del Moral 1979). The factors considered were slope and aspect (measured by Brunton Pocket Transit), position on ridge, substrate, soil development, soil consistency, and snow/drainage patterns.

Voucher specimens were deposited in the University of Idaho Herbarium (ID). Nomenclature follows Hitchcock and Cronquist (1973) except for the Poaceae (Welsh et al. 1987), and *Cymopterus*

TABLE 1.   LIST OF PLANTS USED IN TWINSPAN AND CCA ANALYSES AND ASSOCIATED ABBREVIATIONS DISPLAYED IN GROUP COMPOSITION TABLE (TABLE 1), DENDROGRAM (FIG. 2) AND SPECIES ORDINATION DIAGRAM (FIG. 4). All species were present in at least one plot at greater than 2% cover.

Species	Abbreviations
Achillea millefolium L. var. *alpicola* (Rydb.) Garrett	Ach mil
Agoseris glauca (Pursh) Raf. var. *dasycephala* (T. & G.) Jeps.	Ago gla
Anemone multifida Poir. var. *tetonensis* (Porter) Hitchc.	Ane mul
Antennaria lanata (Hook.) Greene	Ant lan
Antennaria umbrinella Rydb.	Ant umb
Arenaria congesta Nutt. var. *cephaloidea* (Rydb.) McGuire	Are con
Arenaria obtusiloba (Rydb.) Fern.	Are obt
Astragalus kentrophyta Gray var. *implexus* (Canby) Barneby	Ast ken
Calamagrostis purpurascens R. Br.	Cal pur
Carex elynoides Holm.	Car ely
Carex rupestris All.	Car rup
Cymopterus douglassii R. L. Hartman et Constance	Cym dou
Cymopterus nivalis Wats.	Cym niv
Dryas octopetala L. var. *hookeriana* (Juz.) Breit	Dry oct
Elymus spicatus (Pursh) Gould	Ely spi
Elymus trachycaulus (Link) Gould ex Shinners	Ely tra
Erigeron compositus Pursh var. *glabratus* Macoun	Eri com
Eritrichium nanum (Vill.) Schrad. var. *elongatum* (Rydb.) Cronq.	Eri nan
Festuca ovina L. var. *brevifolia* (R. Br.) Wats.	Fes ovi
Frasera speciosa Dougl.	Fra spe
Haplopappus acaulis (Nutt.) Gray	Hap aca
Hymenoxys grandiflora (T. & G.) Parker	Hym gra
Leucopoa kingii (S. Wats.) Weber	Leu kin
Lloydia serotina (L.) Sweet.	Llo ser
Lupinus argenteus Pursh var. *depressus* (Rydb.) Hitchc.	Lup arg
Oxytropis besseyii (Rydb.) Blank. var. *argophylla* (Rydb.) Barneby	Oxy bes
Penstemon attenuatus Dougl. var. *pseudoprocerus* (Rydb.) Cronq.	Pen att
Phlox multiflora A. Nels.	Phl mul
Phlox pulvinata (Wherry) Cronq.	Phl pul
Potentilla diversifolia Lehm.	Pot div
Potentilla ovina Macoun	Pot ovi
Salix nivalis Hook. var. *nivalis*	Sal niv
Selaginella densa Rydb.	Sel den
Silene repens Pers.	Sil rep
Solidago multiradiata Ait. var. *scopulorum* Gray	Sol mul
Synthyris pinnatifida Wats. var. *canescens* (Pennell) Cronq.	Syn pin
Trifolium haydenii Porter	Tri hay
Zigadenus elegans Pursh	Zig ele

douglassii R. L. Hartman et Constance (Hartman and Constance 1985).

Data analysis. To simplify the data analysis, only plants with greater than 2% cover in a particular plot were considered for analysis; in all, 38 species were included (Tables 1 and 2). This simplification is justified because rare species (here defined as having less than 2% mean coverage in a plot) carry an insignificant portion of

TABLE 2. GROUP COMPOSITION TABLE. Group composition with only the 38 species used in the data analysis included. Species abbreviations are explained in Table 1. The eight groups are as follows: (G1) *Salix nivalis*, (G2) *Solidago multiradiata-Trifolium haydenii*, (G3) *Carex elynoides-Trifolium haydenii*, (G4) *Carex elynoides*, (G5) *Calamagrostis purpurascens-Carex elynoides*, (G6) *Carex rupestris*, (G7) *Dryas octopetala*, and (G8) *Leucopoa kingii*. Mean percent cover (C) and frequency of presence in stands (F) are listed for each species. Cover less than 0.5% is indicated by a P.

	G1		G2		G3		G4		G5		G6		G7		G8	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Ach mil			1	100	P	20	P	25	P	7					3	50
Ago gla			P	50			P	6							P	100
Ane mul			P	50			P	6	P	7						
Ant lan					P	20	1	31	P	7						
Ant umb	1	100					1	69	P	37	P	35			P	17
Are con			2	100	P	40	1	38	P	4						
Are obt					1	80	P	69	2	100	1	82			P	33
Ast ken	3	100					P	13	1	44	P	12	1	100	P	33
Cal pur							2	25	14	100	3	94	3	100		
Car ely	15	100			1	60	29	100	14	100	1	35			12	83
Car rup					36	100	1	19	8	85	16	100	7	100	P	17
Cym dou					5	60			P	7	2	76				
Cym niv							1	38	P	22	1	24			2	83
Dry oct													45	100		

TABLE 2. CONTINUED.

	G1		G2		G3		G4		G5		G6		G7		G8	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Ely spi			P	50			2	31			1	6			P	33
Ely tra							P	6								
Eri com							P	13	P	11	P	6			P	67
Eri nan			1	100			P	13	2	78	1	82			P	33
Fes ovi			1	100	P	20	5	44								
Fra spe			3	100	P	20			P	7						
Hap aca									P	4						
Hym gra					P	60	P	19	2	96	P	12			P	33
Leu kin					P	20	P	25	P	7	1	53			19	100
Llo ser	2	100	2	100	P	40	2	44	P	7	P	6	P	50	P	17
Lup arg			2	100			2	50	P	7	P	6	9	100	4	100
Oxy bes							P	25	1	85	1	82			P	17
Pen att							P	25							P	33
Phl mul							1	50								
Phl pul	3	100	4	100	7	100	5	81	7	100	4	94	1	100	5	100
Pot div	3	100	1	50	2	80	1	19	P	4					P	17
Pot ovi					P	20	1	81	1	82					P	33
Sal niv	32	100					1	31	1	41			2	50		
Sel den							P	6							1	33
Sil rep															2	67
Sol mul	7	100	21	100	3	80	P	19	P	7			P	100		
Syn pin	1	50	17	100	3	100	P	63	P	15			P	100	P	67
Tri hay					23	100			P	7	P	6				
Soil	30		39		20		41		43		65		35		49	
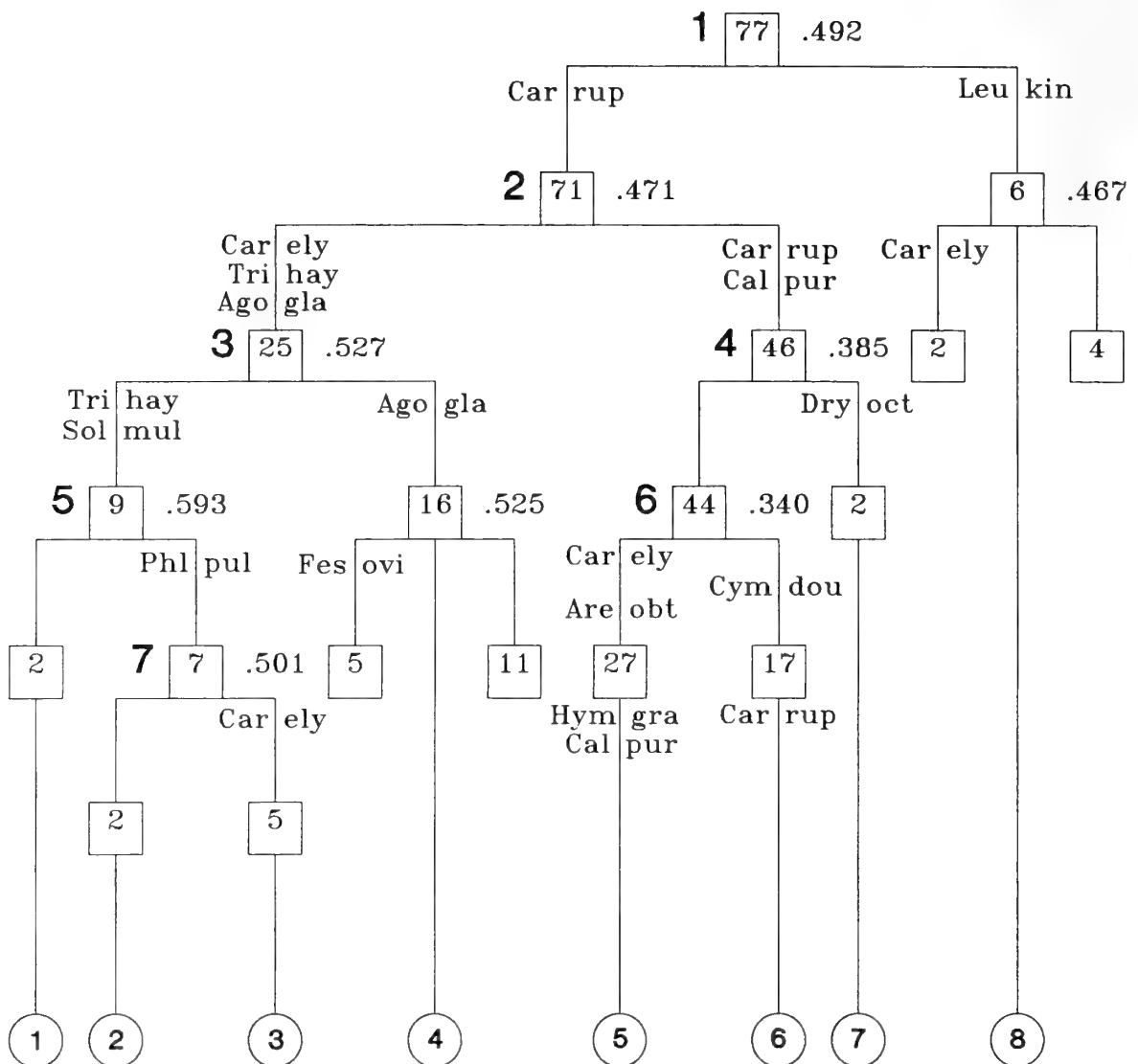
Fig. 2. TWINSPAN dendrogram. Large numbers to the left of boxes are division numbers referenced in the text. Number of plots prior to division is indicated in the box; the eigenvalue associated with the division is to the right of the box. TWINSPAN indicator species (highly preferential to one side of the dichotomy) are shown for each division. Circled numbers refer to group numbers as discussed in the text. (1) *Salix nivalis,* (2) *Solidago multiradiata–Trifolium haydenii,* (3) *Carex elynoides–Trifolium haydenii,* (4) *Carex elynoides,* (5) *Calamagrostis purpurascens–Carex elynoides,* (6) *Carex rupestris,* (7) *Dryas octopetala,* (8) *Leucopoa kingii.*

the information in a plot classification (Gauch 1982). Additionally, this assumption expedited fieldwork since only the 38 species that qualified had to be collected and identified. TWINSPAN (Hill 1979), with default species cutlevels, was used to derive a classification, and canonical correspondence analysis (CCA), as implemented by the program CANOCO (ter Braak 1987–1992) and with species data transformed to the Octave Scale (Gauch 1982), provided an ordination. Both transformations reduce the input of the more abundant species so as to allow the lesser abundant species some influence in the data analysis.

TWINSPAN is a divisive hierarchical classification program using reciprocal averaging repeatedly to divide the data set into smaller and smaller groups (Hill 1979). Analysis was accomplished with the default species cut levels of 0, 2, 5, 10, and 20 percent groupings. The resulting dendrogram was interpreted with respect to field observations and measured environmental variables, with described groups being derived from several levels in the hierarchy.

CCA uses reciprocal averaging constrained by environmental information (ter Braak 1987) to produce axes that are linear combinations of the measured environmental factors. CCA is a kind of reciprocal averaging transformed from an indirect to a direct gradient analysis. An eigenvalue (λ) for each axis indicates the variation of the species data explained by that axis; the larger the eigenvalue, the larger the dispersion of species scores along the axis. When plotted, species scores are derived from the weighted averages of site scores. Arrows in the ordination diagram represent the direction of variation of an environmental variable. The mean of an environmental variable is represented by the origin, so that the direction that the arrowhead points is above average and the opposite direction is below average. The length of the arrow indicates how well the environmental variable is correlated with the pattern in the ordination diagram. Nominal variables or classes (e.g., substrate) are represented as points and are positioned so as to be the weighted average of the site scores of the sites belonging to that class. Each environmental variable also has a correlation coefficient (r) for each axis, which numerically indicates how well that environmental variable helps explain the observed variation on the axis. Overall variation explained by the illustrated ordination is determined by adding the eigenvalues for the axes and dividing by the total of the constrained eigenvalues. Sites perpendicularly projected onto the arrows provide a rank ordering of the sites for that environmental variable. Species are treated in the same manner, except the rank ordering is of the weighted averages of site environmental values of sites containing that species.

RESULTS

TWINSPAN analysis (Fig. 2) of the data set suggests eight groupings: 1) *Salix nivalis,* 2) *Solidago multiradiata–Trifolium haydenii,* 3) *Carex elynoides–Trifolium haydenii,* 4) *Carex elynoides,* 5) *Calamagrostis purpurascens–Carex elynoides,* 6) *Carex rupestris,* 7) *Dryas octopetala,* and 8) *Leucopoa kingii.* The first division (λ = 0.492) separates the *Leucopoa kingii* communities (Group 8) from the rest. The second division (λ = 0.471) primarily distinguishes the more exposed, drier, or steeper sites (Groups 5, 6, and 7) from the more mesic, sheltered sites (Groups 1, 2, 3, and 4). Group 7, *Dryas oc-*
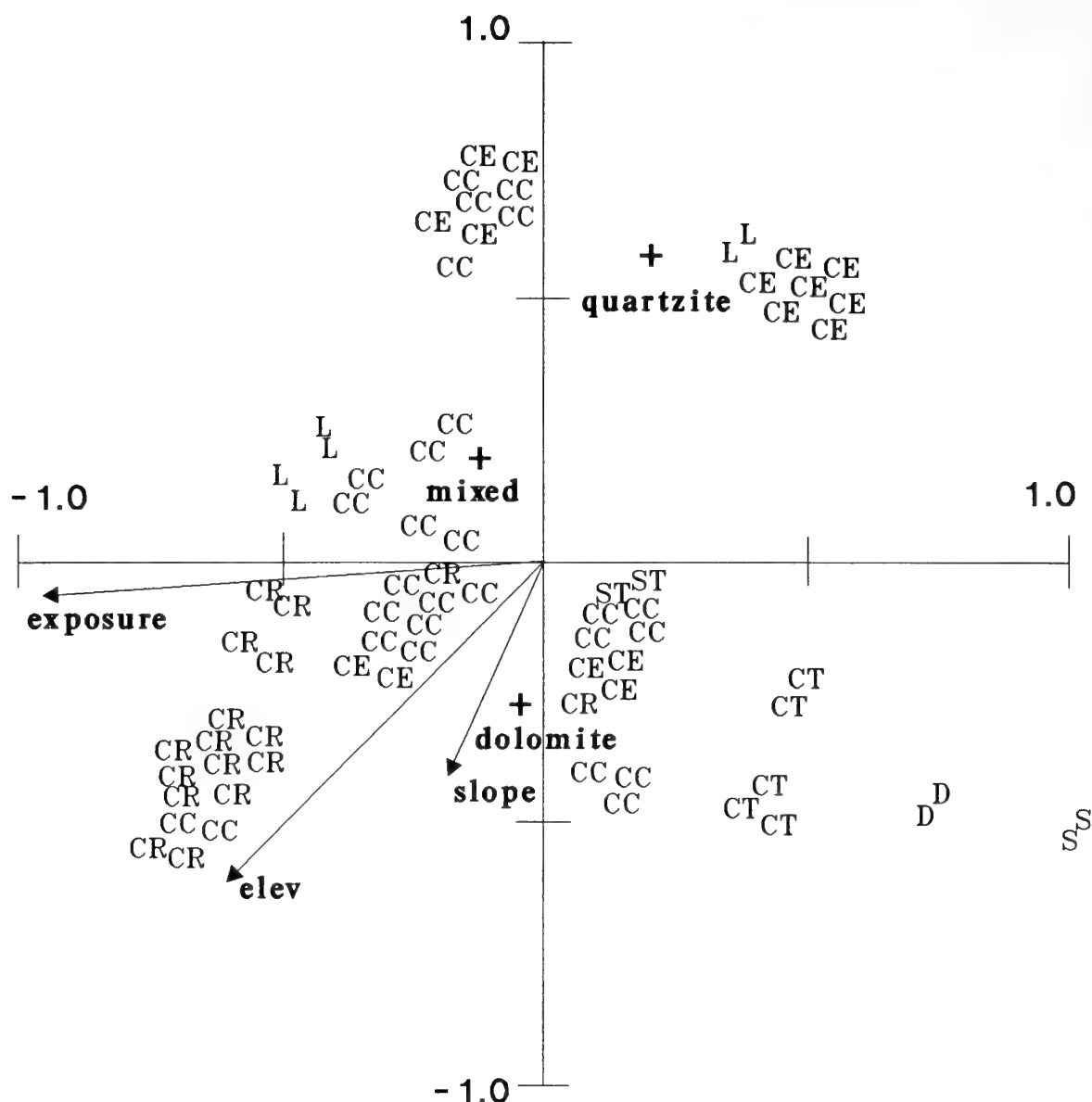
Fig. 3.   CCA ordination of plots. Letters represent community membership. (S) *Salix nivalis*, (ST) *Solidago multiradiata–Trifolium haydenii*, (CT) *Carex elynoides–Trifolium haydenii*, (CE) *Carex elynoides*, (CC) *Calamagrostis purpurascens–Carex elynoides*, (CR) *Carex rupestris*, (D) *Dryas octopetala*, (L) *Leucopoa kingii*.

topetala, is identified as unique at Division 4 by not only having a high composition of *Dryas octopetala,* but also being the only group in which it was found. Division 6 separates the *Calamagrostis purpurascens–Carex elynoides* and *Carex rupestris* communities, but only with the smallest eigenvalue (λ = 0.340) in the dendrogram. Both communities were in exposed, dry locations and had many species in common, most noticeably, *Carex rupestris*. Division 3 (λ = 0.527) is again along an exposure gradient, with the *Carex elynoides* turf community (Group 4) being separated from the less exposed, winter snow-covered or early snowbed communities (Groups 1, 2, and 3). Additional divisions of the latter (Division 5, λ = 0.593; Division 7, λ = 0.501) appear to be associated with date
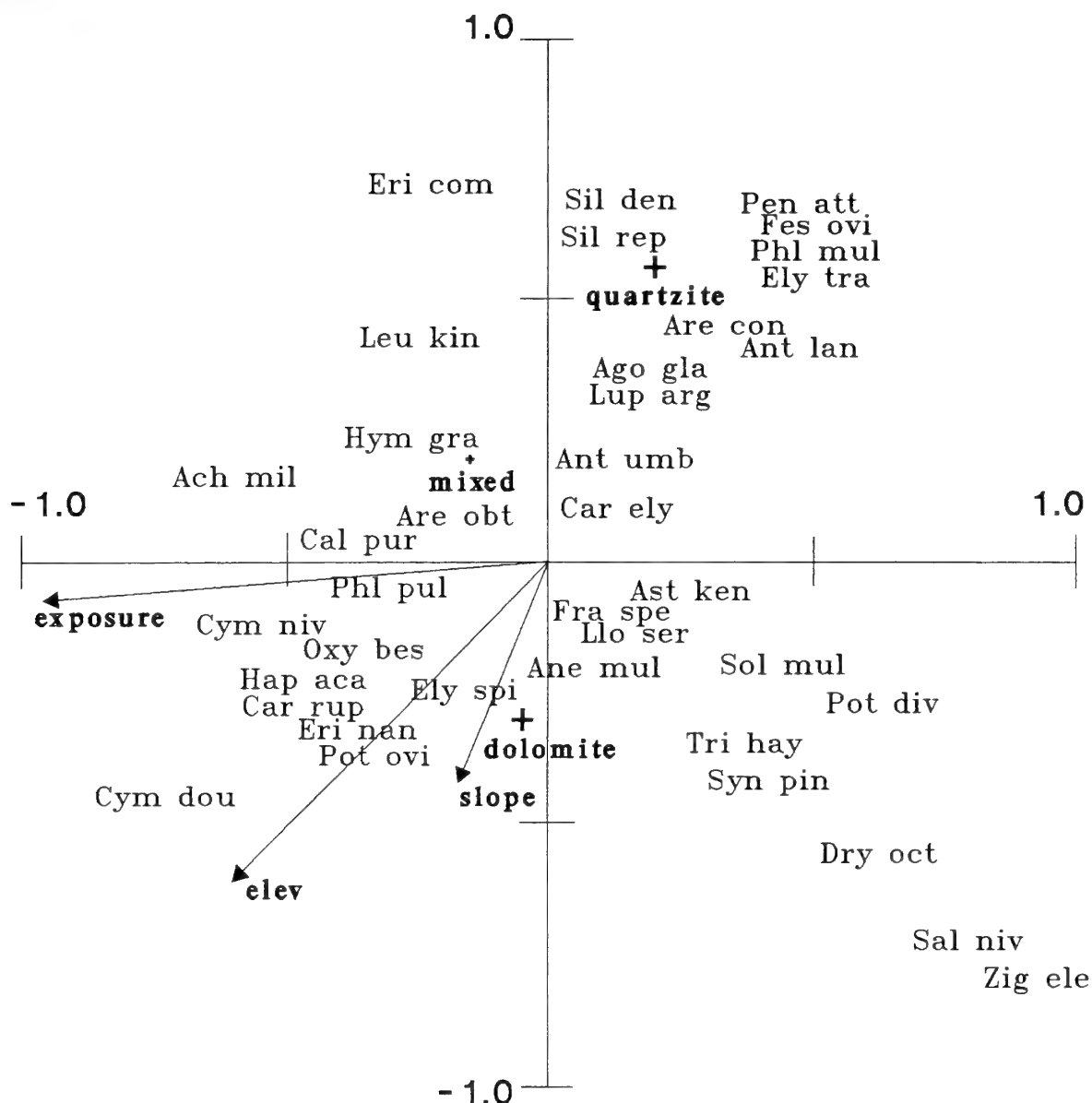
FIG. 4. CCA ordination of species. Species abbreviations are explained in Table 1.

of snowmelt, the *Carex elynoides–Trifolium haydenii* community (Group 3) being free of snow first, followed by the other two (Groups 1 and 2). The *Solidago multiradiata–Trifolium haydenii* community (Group 2) was in an obvious snow-collecting depression, but was free of snow by 21 June. The *Salix nivalis* community (Group 1) was also snow-free, but was fed by an adjacent snowbank.

The CCA ordinations for plots and species are depicted in Figures 3 and 4. The first axis ($\lambda = 0.45$) was correlated primarily with the exposure index ($r = -0.98$), but also partially with elevation ($r = -0.56$). The second axis ($\lambda = 0.30$) was correlated with substrate and elevation ($r = -0.58$). The third axis ($\lambda = 0.22$) was correlated only with slope ($r = 0.92$). Overall, the species and plot ordination diagrams, utilizing the first two axes, display 62.5% of the total variation in all the axes of the CCA ordination (total constrained λ = 1.20).

The plot ordination has the *Salix nivalis* community located in the least exposed, right position, while the *Carex rupestris* community occupies the exposed, left side of the diagram. In between are the remaining communities, which are further differentiated by substrate and elevation. The environmental variables failed to distinguish between two communities, *Carex elynoides* and *Calamagrostis purpurascens–Carex elynoides,* from each other; both communities are concentrated in the middle of the plot and span both substrates. The rest of the communities are well distinguished and will be discussed in detail.

The species ordination also reflects the dominant exposure gradient. *Zigadenus elegans* and *Salix nivalis* var. *nivalis* occupy the extreme right, least exposed position and *Cymopterus douglassii, Achillea millefolium* var. *alpicola,* and *Cymopterus nivalis* occupy the left. The elevation arrow shows *Cymopterus douglassii,* a regional endemic, to be the highest elevation plant collected, while at the opposite extreme is a collection of many species, the most abundant being *Selaginella densa* and *Festuca ovina* var. *brevifolia.* Only *Selaginella densa, Erigeron compositus* var. *glabratus, Penstemon attenuatus* var. *pseudoprocerus, Festuca ovina* var. *brevifolia, Phlox multiflora,* and *Elymus trachycaulus* were collected solely on quartzite. The rest of the species were collected on dolomite or both quartzite and dolomite substrates.

Discussion

Group 1: Salix nivalis (N = 2). This community was located on a shelf (slope = 11°) at the base of a steep ridge, and was clearly associated with persistent snowbanks, drainage from which kept the soil waterlogged during the majority of the growing season (exposure index = 1). Vegetation cover was high (70%) with *Salix nivalis* at 32% ground cover. The location was well-protected from the prevailing westerly winds due to a north-northeast aspect (elevation 3024 m). Soil development was moderate on a dolomite substrate. Other important species present were *Carex elynoides* (15%), *Solidago multiradiata* var. *scopulorum* (7%), *Zigadenus elegans* (4%), *Potentilla diversifolia* (3%), and *Astragalus kentrophyta* var. *implexus* (3%).

From the CCA analysis, the *Salix nivalis* group is the least exposed, wettest community sampled. It has two species, *Salix nivalis* and *Zigadenus elegans,* that occupy the same low exposure position in the species ordination, but the community also contains some species, especially *Carex elynoides,* with more general distributions. This community, and the *Dryas octopetala* community, were the only ones associated with snowbanks still persisting at the time of

sampling. The TWINSPAN divisions (Fig. 2) distinguishing Group 1 from the other mesic sites had high eigenvalues, especially Division 5 (λ = 0.593), highlighting the uniqueness of this community. Group 1 is also characterized by the near absence of the ubiquitous *Phlox pulvinata,* again revealing the extreme mesic nature of the group as compared to the rest of the study area.

Regional studies show *Salix nivalis* communities to be common in east-central Idaho (Brunsfeld 1981), but replaced by *Salix arctica* in the Pioneer Mountains at the western edge of east-central Idaho (Caicco 1983). Brunsfeld's observations support our description of this group as having a mesic habitat preference and occurring in dense mats wherever there is abundant, persistent water. *Salix nivalis* is not mentioned by Moseley (1985), but he was specifically examining *Leucopoa kingii* distributions and discusses other communities only if closely associated with *Leucopoa kingii.*

Group 2: *Solidago multiradiata–Trifolium haydenii* (N = 2). This community was observed in a snow-collecting depression (slope = 3°) on a northwest aspect at 2999 m. Vegetation cover was 61%, with *Solidago multiradiata* var. *scopulorum* at 21% and *Trifolium haydenii* at 17%. The sites were snow-free prior to sampling, and no additional drainage from other snowbanks was evident; the plots were scored a 3 on the moisture index, reflecting average exposure conditions. The soil was moderately developed from a dolomite substrate. Other important species present were *Phlox pulvinata* (4%) and *Frasera speciosa* (3%).

In the TWINSPAN dendrogram (Fig. 2), Group 2 initially branches with Group 3, *Carex elynoides–Trifolium haydenii,* but is separated from Group 3 at Division 7 (λ = 0.501), due mostly to the conspicuous absence of *Carex elynoides.* These two groups were adjacent, and *Carex elynoides* was locally common in the areas around both groups. The absence of *Carex elynoides* suggests an abrupt environmental change, and it is suspected, but not observed, that this is due to a later date of snowmelt in Group 2. Group 3 is more mesic, but this results more from patterns of snowmelt drainage than from snow accumulation.

In the CCA plot diagram (Fig. 3), Group 2 occurs near the centroid for all environmental variables. *Solidago multiradiata* and *Trifolium haydenii* are in the lower right quadrant in the species ordination (Fig. 4), indicating a preference for low exposure, dolomite substrates, and average study area elevations.

Brunsfeld (1981) found *Solidago multiradiata* on rocky, wet soils, and Caicco (1983) discusses a *Deschampsia cespitosa* (L.) Beauv. grassland in which *Solidago multiradiata* occurs with moderate abundance, but no mention is made of a community as described above. *Trifolium haydenii* is a regional endemic known only from southwestern Montana and adjacent Wyoming until recently dis-

covered in east-central Idaho; it occupies a variety of forest and alpine habitats (Henderson 1978).

Group 3: Carex elynoides–Trifolium haydenii (N = 5). This community occupies a north-northwest, relatively steep slope (24°) on dolomite, at an elevation of 3018 to 3060 m. At 80% vegetation coverage, it had the most cover of any group. *Carex elynoides* was present at 36% cover, and *Trifolium haydenii* had 23% coverage. Snow, although not present during sampling, appears to accumulate in large amounts both above and below the community, while the community itself is covered, but not deeply so, in winter. The well-developed soil was wet during sampling; many solifluction terraces were observed. The snow drainage pattern, the high vegetation cover, and the northerly aspect resulted in a score of 2 on the exposure index, indicating a greater than average moisture condition. Other important species were *Phlox pulvinata* (7%) and *Synthyris pinnatifida* var. *canescens* (3%).

The community is positioned in the lower right quadrant of the CCA plot ordination (Fig. 3), indicating low exposure, medium altitude, and a dolomite substrate. The species ordination (Fig. 4) shows *Trifolium haydenii* as preferential to the mesic sites, while *Carex elynoides* has a more general habitat requirement, occurring in all but the driest, most exposed sites.

Other Idaho studies have described *Carex elynoides* as occasional to common, but never in association with *Trifolium haydenii*, a regional endemic (Brunsfeld 1981; Caicco 1983; Moseley 1985).

Group 4: Carex elynoides (N = 16). *Carex elynoides* turf is abundant in the study area. This community occurred on all aspects and on both dolomite and quartzite substrates. The sampling elevation was 3005 to 3054 m, and the mean slope and exposure index were 8.5° and 2.6, respectively. *Carex elynoides* by far dominated the community with 29% coverage, total vegetation coverage being 59%. *Phlox pulvinata* amd *Agoseris glauca* were also important components with 5% and 2%, respectively.

Habitat preference, as revealed in the plot ordination (Fig. 3), tended toward the exposure centroid, but with wide dispersion in substrate and elevation. This community was found in areas not directly exposed to winter winds, with some snow accumulation, moderate slope, and a well-developed soil. The species ordination reveals *Carex elynoides* as a generalist, being located near the centroid. Previous Idaho studies have identified *Carex elynoides* communities as occasional to common, with a habitat preference similar to the above description (Brunsfeld 1981; Caicco, 1983; Moseley, 1985).

A phase of the *Carex elynoides* turf was highlighted by the TWIN-SPAN analysis (Fig. 2) when a small group of five plots was further delimited (λ = 0.525) with *Festuca ovina* var. *brevifolia* as the in-

dicator species. These plots were sampled in depressions or drainage areas and suggests a higher moisture phase of the *Carex elynoides* turf (exposure index = 2), with *Festuca ovina* var. *brevifolia* locally abundant (cover = 16%). *Festuca ovina* is a common species in the alpine of east-central Idaho, but was limited to this community in the study area. Neither Caicco (1983) nor Moseley (1985) mention this phase of a *Carex elynoides* community.

Group 5: Calamagrostis purpurascens–Carex elynoides (N = 27). This community was the largest in total number of plots and total area, and was found on westerly aspects, with an average slope of 12° and elevations from 3005 to 3133 m. The habitat is generally more exposed (average exposure index = 3.4) than *Carex elynoides* turf with *Calamagrostis purpurascens* and *Carex elynoides* each accounting for 14% of the total 57% vegetation coverage. Both dolomite and quartzite substrates are represented, but dolomite predominates. Other important plants were *Carex rupestris* (8%), *Phlox pulvinata* (7%), *Arenaria obtusiloba* (2%), and *Hymenoxys grandiflora* (2%).

In the TWINSPAN analysis (Fig. 2), this group separated early from the other two *Carex elynoides* communities (Division 2, λ = 0.471). It is distinctive because of the large component of *Calamagrostis purpurascens,* as well as *Carex rupestris, Arenaria obtusiloba,* and *Hymenoxys grandiflora,* all four nearly restricted to this community. The CCA plot ordination (Fig. 3) has Group 5 positioned near the centroid for exposure, but widely dispersed relative to the other environmental factors. The environmental variables measured do not distinguish between Groups 4 and 5, but field observations suggest that *Calamagrostis purpurascens–Carex elynoides* plots occurred in the more exposed, drier sites. In fact, on one ridge in the study area, a *Calamagrostis purpurascens–Carex elynoides* community dominated the exposed northwest aspect, while a *Carex elynoides* community was restricted to the partially protected southeast aspect. At its upper boundaries, Group 5 grades into a *Carex rupestris* community (Group 6), which dominates dry, exposed ridgetops. *Calamagrostis purpurascens* is located near the centroid in the species ordination (Fig. 4).

Although Brunsfeld (1981) reported *Calamagrostis purpurascens* to be rare in his alpine study area, collections of the second author and others at ID document it as common, especially on calcareous substrates. Moseley (1985) reported one alpine community in which *Calamagrostis purpurascens* was dominant, but it was not an important component of the alpine communities studied by Caicco (1983).

Group 6: Carex rupestris (N = 17). The *Carex rupestris* community occupied the highest, driest, most exposed sites in the study area. Elevations ranged from 3011 to 3146 m with an exposure index of

3.9. All sites are likely blown snow-free in winter, and all have shallow, rocky soil derived from dolomite. The average slope was 16° but a great deal of variation exists between sites, some occurring on flat ridge tops, while others were on steep inclines. Overall, these communities are sparsely vegetated (35%); most of the area was exposed mineral soil. *Carex rupestris* accounted for 16% of the vegetation coverage, *Phlox pulvinata* 4%, with *Calamagrostis purpurascens* and *Cymopterus douglassii* minor components.

The plot ordination (Fig. 3) further emphasizes the relatively extreme habitat favored by this group, with the *Carex rupestris* plots occurring in the lower left quadrant indicating high exposure, high elevation, and a dolomite-derived soil. The species ordination (Fig. 4) shows *Carex rupestris* in a less extreme position, due to its presence in other communities, but *Cymopterus douglassii* maintains an outlier position. *Cymopterus douglassii* is a highly restricted endemic presently known only from the alpine of the Sheep Mountain RNA and a few alpine/subalpine sites in the vicinity of Mt. Borah, some 47 km southwest in the Lost River Range, Custer County, Idaho. It is only present in the community in the highest elevation sites, while *Calamagrostis purpurascens* becomes more important at lower elevations close to the ecotone between Groups 5 and 6.

Caicco (1983) found only one small example of this community in the Pioneer Mountains, and Moseley (1985) did not encounter it at all in east-central Idaho. This group appears to be rare in Idaho, but it was well-represented in our sampling.

Group 7: Dryas octopetala (N = 2). This community was represented by only two plots in one small area on rocky, dolomitic soil at an elevation of 3048 m. The site is characterized by a steep slope (26°), and a protected, low exposure, northeasterly aspect. The community occurred just below a ridgetop with persistent snowbanks 10 m upslope observed draining through the community (exposure index = 1.5). The vegetation cover was 65% with *Dryas octopetala* var. *hookeriana* accounting for 45%; other important species were *Lupinus argenteus* var. *depressus* (9%) and *Carex rupestris* (7%).

In the plot ordination (Fig. 3), Group 7 is located in the lower right quadrant, indicating a relatively low exposure, dolomite habitat preference. The same preference is evident in the species ordination (Fig. 4), with *Dryas octopetala* exceeded as an outlier by only two other species, *Salix nivalis* var. *nivalis* and *Zigadenus elegans.*

Brunsfeld (1981) collected *Dryas octopetala* in east-central Idaho, and described it as occasional, with a preference for rocky, calcareous substrates and protected, snow-covered ridges, but it was not reported either by Caicco (1983) or Moseley (1985).

Group 8: Leucopoa kingii (N = 6). By species composition, this group was recognized as unique by TWINSPAN (Fig. 2) in the first division (λ = 0.492), with *Leucopoa kingii* communities being sep-

arated from the rest. A subsequent division further indicated two recognizable phases, a stable and an unstable phase, essentially as characterized by Moseley (1985).

The stable phase was found on a mesic, well-developed soil derived from quartzite with moderate slope (12°), an elevation of 3011 m, and a southwest aspect (exposure index = 2). Vegetation coverage was 70%, with *Leucopoa kingii* at 12%; other important species were *Carex elynoides* (34%) and *Lupinus argenteus* var. *depressus* (6%).

The unstable phase was present on a much drier, loose, rocky, dolomite substrate with a steep slope (27°), an elevation of 3036 m, and a west aspect (exposure index = 4). Vegetation coverage was 42%, with *Leucopoa kingii* at 22%; other important species were *Achillea millefolium* var. *alpicola* (4%) and *Cymopterus nivalis* (3%).

The plot ordination (Fig. 3) highlights the differences in the two phases in this group. The stable phase is in the upper right quadrant, revealing a low exposure, quartzite preference, while the unstable phase occupies the lower portion of the upper left quadrant, indicating a high exposure, dolomitic habitat.

Both phases are well-described in Moseley's (1985) investigation of the *Leucopoa kingii* communities of east-central Idaho. Caicco (1983) also observed a few, small *Leucopoa kingii* communities in the White Knob Mountains.

Environmental factors. The measured environmental variables were helpful in describing the community distributions, but did not distinguish between two communities, *Carex elynoides* and *Calamagrostis purpurascens–Carex elynoides*. An exposure gradient, determined by factors such as slope, aspect, snow accumulation/drainage patterns, and soil characteristics, was highly correlated with the first axis and accounted for the majority of the variation observed. Even though the study area has a limited elevation range, elevation was still correlated with both axes 1 and 2 and was helpful in interpreting community and species distributions. Substrate was strongly correlated with the second axis, and accounted for a substantial amount of the variation. Some communities were restricted to one substrate, while others were found on both dolomitic and quartzitic substrates. Caution must be used, however, in interpreting the community substrate preferences; the quartzite bands in the study area are in relatively protected, lower elevation depressions and so represent an environmental contrast to the immediately adjacent dolomite plots, independent of the substrate. Slope was also important, especially in the *Leucopoa kingii* community, and was correlated with the third axis.

Caicco (1983) also describes a "complex moisture-exposure gradient" in his ordinations of central Idaho alpine, as well as a "geographical" axis related to clusters of plots in his large study area. In east-central Idaho, Moseley (1985) again recognized a moisture-

exposure gradient as important. In addition, he identified species composition changes with changes in substrate (limestone vs. non-limestone) and soil stability.

That exposure was found to be important in the distribution of Idaho alpine is no surprise. Billings (1973) clearly describes a "mesotopographic gradient" that explains all the exposure factors found in our study, e.g., slope, aspect, snow accumulation, and drainage. More recently, Isard (1986) thoroughly investigated topographical environmental influences on Niwot Ridge, Colorado, and again, vegetation distribution was found to be dependent on snow accumulation and drainage patterns.

East-central Idaho supports a well-developed, recognizable alpine vegetation. The present study focused on one such alpine site and found eight distinctive communities described on the basis of habitat preference. An exposure gradient was found to be most highly correlated with the observed variation in habitat preferences, but elevation, substrate, and slope were also important. In general, the study area communities present a uniformly dry turf-like physiognomy, with some early snowbed and *Dryas* or *Salix* mat communities occasionally present. This is in sharp contrast to the other regional alpine studies, where fellfields and meadows are also common. Winds, topography, and precipitation patterns appear to be creating a relatively dry alpine habitat; substantial drought stress was obvious at the completion of sampling on 25 July. Drought conditions may help explain the absence of wet meadows, but not the lack of fellfields dominated by cushion plants. These unique features warrant further investigation.

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NOTES

The Habitat and Distribution of *Polemonium chartaceum* (Polemoniaceae) in the Klamath Range: A Clarification.—Daniel W. Pritchett, Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132.

Polemonium chartaceum H. Mason is a small, herbaceous, alpine perennial with showy, head-like inflorescences of dark blue flowers. While the species is known primarily from the White Mountains (Inyo and Mono Cos., California), there are also populations in the Sweetwater (Mono Co., California) and Klamath (Siskiyou and Trinity Cos., California) Mountains.

In the course of a biosystematic investigation of *P. chartaceum* and *P. eximium* E. Greene, the accuracy of published descriptions of the habitat and distribution of *P. chartaceum* in the Klamath Range came into question. The citation of 'subalpine forest ca. 6000' in the Scott Mtns.' by both Grant (Botanical Gazette 150(2):158–169, 1989), the most recent monographer, and Munz (A California flora and supplement, University of California Press, 1973), the reported occurrence on Scott Mountain and the lower elevational limit of 1800 m given in Wilken (*Polemonium,* in The Jepson manual: higher plants of California. ed. J. Hickman. University of California Press, 1993), and 6000' in Grant (1989), and Munz (1973) all may be incorrect. Because *P. chartaceum* is on the California Native Plant Society List IB (Inventory of rare and endangered vascular plants of California, Skinner and Pavlik, 1994) accurate information about habitat and occurrence is essential. In this note results of field and herbarium work are presented that suggest that the descriptions cited above, of habitat and elevational limits, are based on two collections whose locations are erroneous. Revised descriptions of habitat and lower elevational limits are suggested in the discussion which follows.

Locations of *P. chartaceum* populations were noted from herbarium sheets from CAS, F, GH, HSC, JEPS, MO, NY, PH, RENO, RSA, UC, UNLV, US, WTU, the University of California White Mountain Research Station, and the Shasta–Trinity and Inyo National Forests. Location information was obtained also from Horner (unpublished file documents for *P. chartaceum,* California Natural Diversity Database, 1976), Lloyd and Mitchell (A flora of the White Mountains, California and Nevada, University of California Press, 1973), Whipple (A flora of Mt. Eddy, M.A. thesis, Humboldt State University, 1981), and Hunter and Johnson (Madroño 30(4): 89–105, 1983).

In the summers of 1990–1992 all locations (identified from the sources listed above) throughout the entire range of the species were visited. In addition, peaks and ridgelines in the Klamath Mountains in the vicinity of Mt. Eddy were surveyed for undocumented populations of *P. chartaceum.*

All known collections of *P. chartaceum* from the Klamath Mountains are listed in Table 1. Included in the table are collections (*Pritchett 100 and 101*) from two populations discovered in the course of this investigation. Apart from these two populations, *P. chartaceum* has been reported from only three locations in the Klamath Range: 1) the summit of Mt. Eddy, 2) Scott Mountain summit, and, 3) Dobkins Lake. The second and third locations are documented by only single collections. *Lemmon 10,* the sole collection from the Scott Mountain location, consists of only a portion of a single inflorescence.

The habitats of the Mt. Eddy population, the two newly documented Klamath populations, as well as all others in the White and Sweetwater Mountains are characterized by steep slopes, coarse substrates (cobbles and boulders), intense insolation,

TABLE 1.   ALL KNOWN COLLECTIONS OF *P. CHARTACEUM* FROM THE KLAMATH RANGE.

1. *J. G. Lemmon 10,* GH, Scott Mountain, no elevation cited, 1879.
2. *A. A. Heller 13577,* US, NY, Mt. Eddy, 9150 ft, 1917 (original determination *P. shastense* Eastwood).
3. *D. N. Johnson s.n.,* UC, Dobkins Lake, 6000 ft, 1934.
4. *Whipple 960, 1321, 2148,* HSC, Mt. Eddy, 9000 ft, 1979.
5. *S. Horner s.n,* Shasta–Trinity N. F., Crest of the Eddys, no elevation cited, 1979.
6. *M. Denton 4239,* UW, Mt. Eddy, 9000 ft, 1980 (original determination *P. elegans* Greene).
7. *D. Pritchett 100,* CAS, unnamed peak 0.5 mi E Mt. Eddy, 8881 ft (2707 m), 1990.
8. *D. Pritchett 101,* CAS, unnamed peak 1 mi NW Mt. Eddy, 8720 ft (2658 m), 1990.
9. *D. Pritchett 102,* CAS, Mt. Eddy, 9000 ft (2743 m), 1990.

frequent strong winds, and high elevations. In the White Mountains populations are found above 3962 m with scattered individuals as low as 3901 m. In the Sweetwater Mountains, populations are found above 3353 m with scattered individuals as low as 3292 m. Such alpine species as *Erigeron compositus* Pursh, *Hulsea nana* A. Gray, *Hulsea algida* A. Gray, *Ivesia gordonii* (Hook.) Torrey & A. Gray, and *Draba* spp. are often found near the polemoniums, but frequently no other vascular plants are found among the polemoniums at all.

The Scott Mountain summit and Dobkins Lake locations differ from all other *P. chartaceum* locations in several ways. Well defined alpine plant communities are found at neither Scott Mountain summit nor Dobkins Lake. The two locations differ from all other *P. chartaceum* locations also in that they are below latitudinal treeline. Dobkins Lake is surrounded by *Pinus monticola* Douglas forest, while the summit of Scott Mountain is a bald of ultramafic rock surrounded by coniferous forest. No populations of *P. chartaceum* were found at either location during searches in 1990 and 1991, nor are any known to botanists familiar with the area (W. Ferlatte, Siskiyou Co. Dept. Agriculture; J. Nelson, Shasta–Trinity National Forest and B. Williams, Six Rivers National Forest personal communication).

Lemmon 10 is the only known basis of both Munz's and Grant's citings of Scott Mountain as a location. Their decisions to include 'subalpine forest' in habitat descriptions may have been influenced by the low elevation of Scott Mountain (6829 ft) as well.

Johnson s.n. (1934) is the only known basis of the choices of 6000' (Grant 1989; Munz 1973) and 1800 m (Wilken 1993) for the lower elevational limit for the species. Six thousand feet was cited, erroneously, by Johnson, as the elevation for his collection from Dobkins Lake (Dobkins Lake is mapped at 6788 ft on the Mt. Eddy 7.5' quad, provisional edition, 1986, U.S.G.S.). This is the only known association of 6000 ft with a collection of *P. chartaceum.*

The current absence of populations at both Dobkins Lake and Scott Mountain summit, the marked differences between the habitats at these two locations and the habitats of all other known *P. chartaceum* populations, and the existence of only single collections (over a 115 year period) citing these locations suggest that the locations may be erroneous. Specimens of the two collections in question—*Lemmon 10* (1879) and *Johnson s.n.* (1934)—are indistinguishable from those of nearby Mt. Eddy, which is where, in all probability, they were collected.

An explanation of an erroneous citation of Dobkins Lake can easily be imagined: the lake is on an old trail on the slopes of Mt. Eddy and is an obvious place for a campsite. The suggestion of an ascent of Mt. Eddy is strengthened by the actual wording of the description of the location, which reads "Dobkins Lake–Mt. Eddy".

A confusion of Scott Mountain for Mt. Eddy is also plausible. The two peaks are

less than 11 miles apart and are connected by an unbroken summit ridge. Mt. Eddy has been placed in the "Scott Mountains" by some authors, and names for mountains in the area remain unclear even on current maps (Whipple 1981). Collections of other taxa dating from the era of *Lemmon 10* which cite "Scott Mountain" have also led to confusion (W. Ferlatte personal communication).

If the Scott Mountain and Dobkins Lake locations were recorded erroneously there would no longer be reason to consider subalpine forest to be habitat for *P. chartaceum*, nor would there be any reason to place the lower elevational limit of *P. chartaceum* in the Klamath Range at 6000 ft (1800 m); a lower elevational limit based on extant populations would be 2600 m—the lower limit of the newly documented (i.e., *Pritchett 101*) populations near Mt. Eddy.

Another interpretation may be made of the data discussed above. Populations may have existed at Scott Mountain and Dobkins Lake, but became extinct before any botanists besides Lemmon and Johnson saw them. The two locations may contain marginal habitat where populations are re-established at very low rates. This hypothesis is, however, for practical purposes, impossible to test.

All known populations of *P. chartaceum* are found in open, alpine fell fields well above treeline. Unless populations are discovered in subalpine forest, the most plausible explanation of the locations referred to in *Lemmon 10* and *Johnson s.n.* (1934) is, for reasons discussed above, that they were erroneously described. Descriptions of habitat and occurrence of *P. chartaceum* should be revised accordingly.

GALENIA PUBESCENS (AIZOACEAE), NEW TO THE NORTH AMERICAN FLORA.—Timothy S. Ross, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

In June of 1992, while conducting a botanical survey on a site to be developed in Los Angeles County, John Ekhoff, working as a private consultant, encountered an interesting, locally weedy plant which formed low, broadly spreading mounds. The species was common at a portion of the site, so flowering and fruiting material was collected and taken to a couple of individuals who were unable to identify it. Ultimately Mr. Ekhoff brought material to RSA where the prospect of hunting down the plant's identity presented an enjoyable challenge. The author utilized available keys to the angiosperm families and genera while Dr. Robert F. Thorne thought it similar if not identical to a taxon that occurred in Australia. Both eventually arrived at the genus *Galenia*. Fortunately, a monograph of the genus was available (R. S. Adamson, The South African Species of Aizoaceae. III. *Galenia* L., Journal of South African Botany 22:87–127, 1956) and the identity of the collection could be ascertained as *Galenia pubescens* (Ecklon & Zeyher) Druce var. *pubescens*. Given the unusual nature of the find, Mr. Ekhoff returned several days later with a large bag of additional material to be pressed and distributed more widely.

The following two collections from the original discovery site are being distributed (herbarium acronyms follow Holmgren et al., Index Herbariorum, Part I, 8th ed., 1990).

CALIFORNIA. Los Angeles Co.: Signal Hill, disturbed, undeveloped property along Hill Street in the two-block area between Stanley and Ohio Avenues, locally

common herbaceous to suffrutescent perennial, forming low mounds or mats 10–30 dm in diameter, elevation ca. 250 ft (76 m), Long Beach USGS 7.5′ Quadrangle T4S R12W Section 29, 5 June 1992, *J. Ekhoff, s.n.* (RSA [2 sheets], UC); same location, 12 June 1992, *J. Ekhoff, s.n.* (RSA, AD, ARIZ, CAS, CDA, GH, K, MO, NY, OSU, RM, TEX, UCR, UCSB, US).

The genus *Galenia* comprises ca. 27 species with a natural distribution restricted to southern Africa. There it is particularly characteristic of the west and south-west, especially along the margins of the Karoo, although some taxa occur along the southern coastal belt. All the taxa are lowland plants and are apparently absent from the main summer-rainfall areas. Two of the taxa, *G. secunda* (L.*f.*) Sonder *in* Harvey and *G. pubescens* var. *pubescens*, are now naturalized weeds in lowland areas of southern Australia (A. Prescott *in* A. S. George [ed.], Flora of Australia, Vol. 4, pp. 50, 52, 1984). *Galenia secunda*, the first and only other species of the genus recorded in the North American flora, was apparently reported by Clewell from the Florida panhandle (John W. Thieret personal communication). It is interesting to note that, of the 27 species in the genus, the two now collected in North America are the same two taxa that occur as weeds in southern Australia.

There are two known herbarium specimens documenting that *G. pubescens* var. *pubescens* was cultivated previously at the U.S. Fire Lab at the University of California, Riverside. These sheets are deposited at UCR (U.S. Fire Lab, UCR; nursery-grown; seeds from Australia; *Eamor C. Nord, s.n.,* 29 July 1970) and CDA (same location; *E. C. Nord, s.n.,* 29 January 1971). According to Andrew C. Sanders, Curator of the UCR herbarium (personal communication), Mr. Nord was interested in fire-resistant plants, particularly those that grew as groundcovers, and consequently cultivated a diversity of unusual taxa in the course of his studies. Despite the fact that this taxon has been cultivated in Southern California, however, there appears to be no evidence suggesting a link between the material grown at Riverside in the 1970's and the plants encountered as weeds at Signal Hill, which may have arrived at the site via independent means.

This taxon is adapted to low-elevation areas with a winter-rainfall regime and long, dry summers, and can be quite tenacious once established. Adamson (1956) indicates that in southern Africa this species has been utilized as a fodder plant during periods of drought. Its resilience is amply demonstrated at Signal Hill where, according to Mr. Ekhoff, plants are mowed on a fairly regular basis but continue to flourish, and a portion of the site that has been plowed is still infested (personal communication, Feb. 1994). A single, well-established plant may also produce hundreds (if not thousands) of seeds in a single season. Needless to say, an alien species with these characteristics has the potential to become a serious weed in lowland regions of the Pacific U.S. Although the currently known site is land-locked in suburbia, it is unclear whether the proposed development at the Signal Hill locale will result in the extirpation of this potentially pernicious weed. Due to the species' adaptability and tenacious demeanor once established, botanists and agricultural agents should watch carefully for it when working in the field in order to prevent its establishment elsewhere in the region.

Since the taxon has not previously been recorded in North American floras, the following descriptive information is provided, adapted from Adamson (1956) and Prescott (1984):

Galenia L. (Species Plantarum 1:359, 1753. Genera Plantarum 5th ed., 169, 1754. Type species, *G. africana* L. Named for Claudius Galenius, Roman physician and writer on medicine ca. 130–200 A.D.). The genus is characterized by exstipulate leaves, small flowers, a superior ovary with a single pendulous ovule in each carpel, and stamens twice as many as the perianth segments and arranged in pairs alternating with the perianth lobes. Two subgenera are recognized: Subgen. *Galenia* (6 spp.), erect or suberect shrublets with opposite, linear or linear-oblong (sub-) glabrous leaves, 4-merous perianths, 2 styles, and fruits not or tardily dehiscent; and Subgen. *Kolleria* (Presl) Fenzl emend. Adamson (21 spp.), to which the two North American adventives

belong. This latter subgenus consists of prostrate or diffuse shrublets; leaves usually secund, opposite or alternate, most commonly obovate or spatulate and commonly gray or whitish; flowers in secund or cymose inflorescences; perianth segments 4 or 5, usually alike; styles 2–5; and fruit dehiscent.

Galenia pubescens (Ecklon & Zeyher) Druce var. *pubescens* (Botanical Society and Exchange Club of the British Isles 1916:624, 1917). Suffrutescent perennial, forming green or grayish patches 1 m or more across. Stems procumbent, 2.5–15 dm long, much branched. Young parts with closely appressed rather coarse hairs, the older glabrescent. Leaves alternate, papillose; those on the main shoots broadly obovate-spatulate, 5–22 mm long, 2–20 mm wide, obtuse or subobtuse, narrowed at the base, often falling at about flowering time; those on lateral branches smaller, more acute, often concave above. Flowers on alternate secund lateral branches 2–8 cm long, either distant or crowded, and often themselves branched. The flowers solitary or with a pair of branchlets from the base 1–3 mm long, each bearing 1–3 flowers. Bracts similar to the leaves but smaller, less narrowed at their bases. Perianth segments generally 5, 2–3 mm long by ca. 1 mm broad, pubescent with closely appressed hairs outside, white to pinkish inside; anthers usually pink (pale salmon-pink in the Signal Hill material). Capsule conspicuous, 2.5–3 mm wide, 1 mm long, persistent with leaf bases. Seeds ca. 1.2–1.4 mm long, subreniform-ovate in profile, glossy black (reddish-brown when immature), striate dorsally, the striations broken and somewhat tuberculate laterally.

NOTEWORTHY COLLECTIONS

ARIZONA

LEPIDIUM LATIFOLIUM L. (BRASSICACEAE).—Coconino Co., Grand Canyon National Park, Colorado River Mile (CRM) 37 [below Lees Ferry], Tatahatso Wash pool at base of wash and outflow, 30 July 1978, *Gloria Hardwich Griffith s.n.* (MNA).

Previous knowledge. An eastern Mediterranean weed that has been spreading in the U.S. from east to west, it occurs in Utah and California. The closest published population in Utah is in Washington Co. (Albee et al., Atlas of the Vascular Plants of Utah, 1988), although it is more common along the Wasatch Front and tributaries into the Green River in northeastern Utah. It should be looked for in the Green and Colorado river drainages in southeastern Utah and additional tributaries of the Colorado in the Grand Canyon.

Significance. The MNA specimen represents the first collection from Arizona (misidentified as *L. medium*) and may document the site of introduction. This species is rapidly colonizing moist sandy beaches and channel margin habitats along the length of the Colorado River in Grand Canyon National Park. In the past two years it has been documented from numerous additional sites: CRM 24.5, 34–36, 43, 51.5, 56, 59, 71, 74, and 194 [duplicate verified by I. Al-Shebaz (MO)]. Specimens from these locations are deposited at ASC. The plants are long-lived perennials that reproduce by rhizomes as well as setting hundreds of seeds that become mucilaginous and sticky

when wetted. In the near future, *L. latifolium* could become the dominant vegetation along the lower riparian zone in the Colorado River corridor.

—TINA AYERS, Northern Arizona University, Biological Sciences Department, P.O. Box 5640, Flagstaff, AZ 86011 and LAWRENCE E. STEVENS, Resources Management Division, Grand Canyon National Park, Grand Canyon, AZ 86023.

MONTANA

BRAYA HUMILIS (C. A. MEY.) ROBINS. (BRASSICACEAE).—Beaverhead Co., Pioneer Range, Lion Mtn., 12 km S of Wise River, locally common in dolomite-derived soil on a gentle S-facing slope with *Dryas octopetala* and *Saxifraga oppositifolia,* T3S R11W S3, 2865 m, 25 Jul 1991, *P. Lesica and S. V. Cooper 5532* (MONTU, GH). Verified by R. H. Rollins (GH).

Significance. First report for Montana, 650 km S of the nearest station in SW Alta and 1000 km NW of disjunct populations in c. Colorado.

CAMISSONIA PARVULA (NUTT.) RAVEN (ONAGRACEAE).—Carbon Co., Pryor Mtns. Desert, 3 km E of Bear Canyon, uncommon in sand at the edge of calcareous outcrops at the mouth of a small drainage with *Phacelia ivesiana* and *Streptanthella longirostris,* T9S R26E S10 NE¼, 1570 m, 12 Jun 1991, *P. Lesica 5406* (MONTU); ca. 2 km W of Gypsum Creek, local in sandy soil at the edge of a small drainage with *P. ivesiana* and *Gilia inconspicua,* T9S R26E S12 SW¼, 1615 m, 12 Jun 1991, *P. Lesica 5408* (MONTU, NY). *Lesica 5408* verified by A. Cronquist (NY).

Significance. First report for Montana, an extension of 120 km N from Washakie Co., Wyoming.

CHAENORRHINUM MINUS (L.) LANGE (SCROPHULARIACEAE).—Flathead Co., along Hwy 2 ca. 8 km E of West Glacier, locally common in gravelly soil beneath cottonwoods with *Agrostis alba* and *Crepis tectorum,* T32N R18W S34, 1035 m, 10 Jul 1991. *P. Lesica 5484* (MONT, NY); Lincoln Co., on the banks on Lake Koocanusa (reservoir), common in moist sandy soil with *Matricaria matricarioides* and *Polygonum aviculare,* T36N R28W S1, 775 m, 16 Jul 1992, *P. Lesica 5786* (MONTU); Missoula Co., Stickney home on the W side of Rattlesnake Creek Valley ca. 1.5 km NNE of Missoula, adventive in domestic flower garden, T31N R19W S14, 1020 m, 10 Jul 1976, *P. F. Stickney 3418* (MRC, ID, MONT, MONTU, WS, USFS/RM). *Lesica 5484* verified by A. Cronquist (NY); *Stickney 3418* determined by M. P. Widrlechner.

Previous knowledge. Since first recorded in 1874 at Camden, New Jersey this southern European species' discontinuous and at times rapid spread across transcontinental Canada and e. U.S. has been associated with railroads (Arnold, Natural History 90(8): 58–65, 1981; Widrlechner, *Canadian Journal of Botany* 61:179–187, 1983; Moss & Packer, *Flora of Alberta* 2nd edition, 1983; Great Plains Flora Association, *Flora of the Great Plains,* 1986). The earliest known station near Montana was detected sometime between 1940 and 1974 and reported by Taylor for the extreme SE corner of British Columbia (*The Figwort Family Scrophulariaceae of British Columbia,* B.C. Provincial Museum Handbook No. 33, 1974). This location is approximately 80 km NW of *Lesica 5484* and 30 km ENE of *Lesica 5786.* Occurrences in e. Washington, w-c. Idaho and ne. Oregon were recently reported by Old et al. (*Madroño* 40:136, 1993).

Significance. First report for Montana; not listed in *Flora of Montana Part 2* (Booth & Wright 1966) or *Vascular Plants of Montana* (Dorn 1984). *Lesica 5484* is in the vicinity of a transcontinental railroad. *Stickney 3418* appeared abruptly in a spring bulb garden, possibly introduced with potted bedding plants. Since 1976 it has remained within the yard and its ability to disperse locally appears limited.

CRYPTANTHA SCOPARIA A. NELSON (BORAGINACEAE). — Carbon Co., Pryor Mtns. Desert, 6 km N of Frannie, Wyoming, locally common in sandy soil on an upper E-facing slope of a low ridge with *Gilia leptomeria* and *Lappula redowskii,* T9S R25E S24 SW¼, 1370 m, 11 Jun 1991, *P. Lesica 5391* (MONTU, MONT); same location, 28 Jun 1991, *P. Lesica 5469* (MONTU, NY). *Lesica 5469* verified by A. Cronquist (NY).

Significance. First report for Montana, an extension of 320 km N from Sweetwater Co., Wyoming and ca. 360 km NE from s. Idaho.

ERIOGONUM SALSUGINOSUM (NUTT.) HOOK. [=*STENOGONUM SALSUGINOSUM* NUTT.] (POLYGONACEAE). — Carbon Co., Pryor Mtns. Desert, ca. 1 km N of McKown Well, abundant in bentonitic soil of badlands toeslopes with *Allium textile* and *Halogeton glomeratus,* T9S R26E S27, 1450 m, 11 Jun 1991, *P. Lesica 5387* (MONTU); same location, 24 Jun 1991, *P. Lesica 5435* (MONTU).

Significance. First report for Montana, an extension of 120 km N from Washakie Co., Wyoming.

ERIOPHORUM CALLITRIX CHAM. (CYPERACEAE). — Carbon Co., Beartooth Mtns., near Hwy 212 just W of Wyoming Creek, common in wet tundra at head of a small creek with *Salix planifolia* and *Carex scopulorum,* T9S R19E S20 SW¼, 2985 m, 15 Aug 1991, *P. Lesica 5585* (MONTU, NY); Line Creek Plateau, uncommon in wet turf at the head of a small drainage, with *S. planifolia* and *C. scopulorum,* T9S R19E S27, 3050 m, 16 Aug 1991, *P. Lesica 5591* (MONTU, NY). Verified by A. Cronquist (NY).

Significance. First record from Montana; previously known from adjacent Park Co., Wyoming.

HAPLOPAPPUS CARTHAMOIDES (HOOK.) A. GRAY VAR. *SUBSQUARROSUS* (GREENE) DORN (ASTERACEAE). — Carbon Co., Beartooth Mtns., along North Line Creek below Line Creek Plateau, common in limber pine woodland with *Artemisia tridentata* and *Agropyron spicatum,* T9S R20E S21, 2195 m, 6 Aug 1993, *P. Lesica 6185* (MONTU, RM); along Robertson Draw below Line Creek Plateau, common in grasslands with *Agropyron spicatum* and *Stipa comata,* T9S R20E S27, 1845 m, 6 Aug 1993, *P. Lesica 6186* (MONTU). Verified by R. Dorn (RM).

Significance. First report for Montana; previously known only from adjacent Park Co., Wyoming. Currently a candidate for listing as a threatened or endangered species by U.S.F.W.S.

KALMIA POLIFOLIA WANG. VAR. *POLIFOLIA* [=*K. OCCIDENTALIS* SMALL] (ERICACEAE). — Flathead Co., Glacier National Park, along the W edge of McGee Meadows, locally common in *Sphagnum* moss at the periphery of a spruce forest with *Ledum glandulosum* and *Potentilla palustris,* 1190 m, 17 May 1993, *P. Lesica 5901* (MONTU, NHA); Numa Ridge ca. 3 km NE of foot of Bowman Lake ca. 9 km NE of Polebridge, common on hummocks in a *Sphagnum* bog with *Ledum glandulosum* and *Lycopus uniflorus,* 1525 m, 24 Aug 1986, *P. Lesica and A. DeBolt 4105* (MONTU); Missoula, Co., Bitterroot Mtns., Mary's Frog Pond 31 km SW of Missoula, common to lake shore margin with *Ledum glandulosum* and *Sphagnum* sp., T11N R22W S15, 1750 m, 25 May 1969, *P. F. Stickney 1830* (MRC, MONT, USFS/RM); same location, 14 May 1987, *R A. Petty 64* (MONTU); Jocko Mtns., Sheep Mtn. Bog 18 km ENE of Missoula, slightly raised areas of bog margin with *Ledum glandulosum,* T14N R17W S19, 1920 m, 17 Oct 1981, *P. F. Stickney 4085* (MRC, USFS/RM); Ravalli Co., Bitterroot Mtns., Lower Twin Lake at headwater of Lost Horse Creek, moist site at margin of subalpine forest, T5N R23W S29, 1980 m, 23 Aug 1959, *P. F. Stickney s.n.* (MRC). *Lesica 5901* verified by G. Crow (NHA); *Stickney 1830* determined by C. Feddema (USFS).

Significance. First report for Montana and the Northern Rocky Mountains; an extension of 800 km S from n. Alberta and 550 km E from w. Washington.

LOMATIUM ATTENUATUM EVERT (APIACEAE).—Beaverhead Co., Tendoy Mtns., side canyon N of Limekiln Canyon, common in limestone talus on a steep SW-facing slope, T11S R11W S1, 1920 m, 8 Jun 1993, *P. Lesica 5990* (MONTU, RM).

Significance. First report of this newly described species (Evert, *Madroño* 30:143–146, 1983) for Montana; previously known only from Park Co., Wyoming.

MIMULUS BREVIFLORUS PIPER (SCROPHULARIACEAE).—Flathead Co., Glacier National Park, along the trail above Ole Creek, locally common in open soil of SE-facing slopes with *Collinsia parviflora* and *Epilobium minutum*, T29N R16W S13, 1220 m, 1 Jun 1992, *P. Lesica 5664* (MONTU); above Ole Creek 4 km E of Walton, local on wet moss on large rock outcrops with *Epilobium minutum* and *Arenaria serpyllifolia*, T29N R15W S7 SW¼, 1280 m, 3 Jun 1993, *P. Lesica 5980* (MONTU). *Lesica 5664* verified by R. Meinke (OSC).

Significance. First report for Montana, an extension of 240 km E from n. Idaho.

NAMA DENSUM LEM. VAR. *PARVIFLORUM* (GREENM.) HITCHC. (HYDROPHYLLACEAE).—Carbon Co., Pryor Mtns. Desert, 1 km SE of mouth of Bear Canyon, local in sand at the edge of calcareous sandstone outcrops with *Phacelia ivesiana* and *Gilia leptomeria*, T9S R26E S9 NE¼, 1540 m, 12 Jun 1991, *P. Lesica 5403* (MONTU, NY). Verified by A. Cronquist (NY).

Significance. First report for Montana.

PEDIOCACTUS SIMPSONII (ENGELM.) BRITTON & BROWN (CACTACEAE).—Beaverhead Co., N of Sheep Corral Gulch 8 km S of Bannack, uncommon and local in sagebrush steppe with *Agropyron spicatum* and *Eriogonum ovalifolium*, T8S R12W S16, 1875 m, 3 Jul 1991, *P. Lesica 5473* (MONTU, NY, BYU). Verified by S. L. Welsh (BYU).

Significance. First report for Montana, a range extension of 60 km E from Lemhi Co., Idaho. This species has now been collected from at least six other locations in s. Beaverhead Co.

POA CURTA RYDB. (POACEAE).—Carbon Co., Pryor Mtns., basin at the head of Layout Creek, common in Douglas-fir forest with *Arnica cordifolia* and *Solidago spathulata*, T8S R28E S33, 2040 m, 19 Jun 1992, *P. Lesica & R. DeVelice 5704* (MONTU, UT). Determined by Lois Arnow (UT).

Significance. First report for Montana, previously known from adjacent Park Co., Wyoming.

SATUREJA ACINOS (L.) SCHEELE (LAMIACEAE).—Powell Co., 1 km N of Tupper Lake, locally common in gravelly soil at the edge of an old logging road with *Centaurea maculosa* and *Filago arvensis*, T15N R10W S30, 1400 m, 29 Jul 1993, *P. Lesica 6136* (MONTU, NHA). Verified by G. Crow (NHA).

Significance. First report of this introduced species for Montana and the Northern Rocky Mountains.

SAXIFRAGA HIRCULUS L. [=*HIRCULUS PROPREPENS* (FISCH.) LOVE AND LOVE] (SAXIFRAGACEAE).—Carbon Co., Beartooth Mtns., along the stream feeding into Crescent Lake on the Hellroaring Plateau, uncommon in wet, organic soil of an alpine fen, T9S R18E S15, 3110 m, 8 Aug 1993, *P. Lesica 6190* (MONTU, CO). Verified by W. A. Weber (CO).

Significance. First report for Montana and the Northern Rocky Mountains; an extension of 2300 km S from n. British Columbia and 500 km N from disjunct populations in Utah.

—PETER LESICA, Herbarium, Division of Biological Sciences, University of Montana, Missoula, MT 59812 and PETER F. STICKNEY, USDA Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, P.O. Box 8089, Missoula, MT 59807.

OREGON

Carex whitney Olney (Cyperaceae). — Wasco Co., partial shade of open *Pinus contorta*, with *Carex rossii, Penstemon euglaucus, Fragaria virginiana*, edge of USFS hiking trails 468 & 469, headwaters of Little Badger Cr., 19 km ESE of Mt. Hood summit, 1540 m, Badger Cr. Wilderness, Mt. Hood National Forest; T3S R11E S8 SE¼ of SW¼; 29 July 1991; *Zika 11311* (OSC).

Previous knowledge. Northern limit of range reported as Crater Lake National Park, Klamath Co., according to collections at OSC, ORE, WILLU, and Howell (Leaflets of Western Botany 8:220–224, 1958). Endemic to Oregon and California. Although common in the California Sierra it is rare in Oregon, where it was last collected in 1936 (Oregon Natural Heritage Program, Rare, Threatened and Endangered Plants and Animals of Oregon, ONHP, Portland, 1993). Surveys for the species in 1993, funded by a grant from the Crater Lake Natural History Association, showed it is extant in Crater Lake National Park.

Significance. Northern range extension in Cascade Mts. by 270 km from Crater Lake.

—Peter F. Zika, Herbarium, Department of Botany, Oregon State University, Corvallis, OR 97331.

YUKON

Botrychium multifidum (Gmel.) Rupr. var. *multifidum* (Ophioglossaceae). — Yukon Territory, southeast of Dawson along Rt. 2; 63°56′25″N, 138°30′59″W; growing in old gravel road bed, ca. 0.5 km east of Rt. 2; old road cut bisected a *Populus tremuloides/Picea glauca* stand; ca. 683 m, 24 July 1993, *Robert W. Lichvar and Catherine E. Kennedy 7915* (DAO), Det. William J. Cody. After a short search, only 2 individuals were located growing in the abandoned gravel road bed.

Previous knowledge. Raup reported *B. multifidum* from Fort Simpson, District of Mackenzie, Northwest Territories, ca. 900 km SE, but did not specify which variety (Raup, The Botany of Southwestern Mackenzie, Sargentia 6, 1947). Cody (1993) determined this collection to be var. *multifidum* (*Raup and Soper 9917*, GH, photo DOA). Cody reported var. *multifidum* from Fort Smith on the Alberta–District of Mackenzie border some 550 km farther SE (Cody, The Canadian Field-Naturalist 70(3):101–130, 1956). Taylor stated that nearly all plants in the Alaskan Panhandle, British Columbia and southward belonged to var. *intermedium* (D. C. Eat.) Farw. but did not distinguish the varieties on his map (Taylor, Pacific Northwest Ferns and Their Allies, University Toronto Press, 1970). The nearest location in the Alaskan Panhandle is ca. S. Hultén reported ssp. *robustum* (Rupr.) Clausen (=var. *intermedium*) from the eastern Aleutian Islands, Alaska, ca. 1175 km SW (Hultén, Flora of Alaska and Yukon, Lunds Universitets Årsskrift N.F., Avd., 2, 37:1, 1941). One collection of var. *multifidum* has been made near Fairbanks, Alaska, ca. 350 km NW (*A. Bierman s.n.*, ALA, photo DAO) and one collection of var. *intermedium* has been made on Evans Island, Alaska, ca. 650 km SW (*E. Bishop 1902*, ALA, photo DAO), both determined by Cody (1993).

Significance. First record for *B. multifidum* var. *multifidum* in the Yukon Territory, Canada. The distribution map in Cody and Britton (Ferns and Fern Allies of Canada, Agriculture Canada, 1989) for all varieties was based largely on DAO and CAN collections, missed the Raup specimen at Gray Herbarium for Fort Simpson, Northwest Territories. *Botrychium multifidum* var. *multifidum* should be added to the list of rare plants of the Yukon (Douglas et al., The Rare Plants of the Yukon, Syllogeus 28, 1981).

—ROBERT W. LICHVAR, US Army Engineer Waterways Experiment Station, 3909 Halls Ferry Road, Vicksburg, MS 39180 and WILLIAM J. CODY, Agriculture Canada, Centre for Land and Biological Resources Research, Wm. Saunders Building, C.E.F., Ottawa, Ontario K1A 0C6.

ANNOUNCEMENT

RANCHO SANTA ANA BOTANIC GARDEN
NAMES NEW EXECUTIVE DIRECTOR

Rancho Santa Ana Botanic Garden at Claremont, CA—The Trustees of Rancho Santa Ana Botanic Garden have named Dr. Roy L. Taylor Executive Director effective November 1, 1994.

Dr. Taylor, currently President and Chief Executive Officer for the Chicago Horticultural Society and Director of The Chicago Botanic Garden, is nationally recognized for his contributions to botany, horticulture and the role of botanic gardens in public education and conservation.

Born in Alberta, Canada, Dr. Taylor received his B.S. in Biology at Sir George Williams University, Montreal, and later pursued his doctorate at the University of California, Berkeley where he completed his Ph.D. in Botany. His professional experience includes research and university faculty positions, most recently at the University of Illinois. Prior to his appointment in Chicago in 1985, he was Director of the Botanical Garden and Professor of Botany at the University of British Columbia. From 1965–1968 he was Chief of the Taxonomy and Economic Botany Section for Canada Agriculture in Ottawa.

Dr. Taylor has published widely, authoring the *Flora of the Queen Charlotte Islands* with James A. Calder in 1968, and has served as editor and contributor to over 150 scholarly and horticultural journals. He was the recipient of the Queen's Silver Jubilee Medal in 1977, The George Robert White Medal of Honor from the Massachusetts Horticultural Society in 1986 and the American Association of Botanic Gardens & Arboreta Award of Merit in 1987. He has been involved in many professional organizations and served as Director and later President of AABGA. From 1980 to 1993 he contributed extensively of his talent and time to the American Association of Museums where he served as Chairman of the Accreditation Commission, as well as the first Chairman of the Ethics Commission. Dr. Taylor is also a member of American Society of Plant Taxonomists, Botanical Society of America, International Association of Botanical Gardens, Linnean Society of London, and Fellow of the Royal Horticultural Society. He is founding Trustee of Botanic Gardens Conservation International of Kew, England.

OBITUARIES

John Thomas Howell
1903–1994

John Thomas Howell, Curator Emeritus of Botany at the California Academy of Sciences, died at his home in Marin County, California on 7 May 1994. Tom had served as both Secretary (1930, 1931) and Vice President (1955) of the California Botanical Society. Tom was born in Merced, California and by the time he entered high school there, he had become particularly interested in plants. He studied botany under W. L. Jepson at the University of California at Berkeley and received his M.A. in 1927. From 1927–1929, Tom was the first resident botanist at the Rancho Santa Ana Botanic Garden when it was still located on Susanna Bixby Bryant's ranch in Santa Ana Canyon. In 1929, Alice Eastwood offered Tom a position in the herbarium at the California Academy of Sciences where he spent the next 65 years in botanical exploration, research, and public education. Although Tom collected nearly 55,000 plants, mostly from throughout California and the western United States, tropical botanists recognize his enormous contributions to the study of the Galapagos Islands flora. From March to September of 1932, Tom was a botanist on the Templeton Crocker Expedition to the Galapagos where he collected 1627 plants on 14 of the islands. These collections formed the basis for some of the first serious revisionary studies of plant groups with significant radiation in the Galapagos Islands. Tom's publications on the Galapagos flora dealt with such groups as *Mollugo,* Cactaceae, Amaranthaceae, *Tiquilia, Scalesia,* and *Polygala.* In California, Tom collected plants in the Sierra Nevada for some 25 years with the prospect of writing a flora of that mountain range. The 20 herbarium cases housing specimens generated by those efforts are now being incorporated into the Academy's herbarium. Because they were largely unmounted, Howell's Sierran plants were not readily accessible for use by authors of the recent *The Jepson Manual.* Botanically, Tom was a generalist with a particular interest in regional floras. Plants named for Tom include an alga, a fungus, a lichen, a liverwort, a moss, monocots, and dicots. His "specialties" included the Asteraceae, Cyperaceae, Hydrophyllaceae, Poaceae, Polygonaceae, Rhamnaceae, and Rubiaceae. His bibliography includes more than 500 entries, most of which deal with California plants. He considered his editing and publication of the private journal *Leaflets of Western Botany* (10 volumes and index, 1932–1968) to be his most important contribution to California botany. Another of Tom's best known and most popular publications is *Marin Flora, Manual of the Flowering Plants and Ferns of Marin County, California.* Although Tom did not teach in a university classroom setting, he probably taught botany to nearly as many people as most college professors. His students included Junior Academy schoolchildren, Sierra Club chapters, the California Native Plant Society, and California Botanical Club. Tom served as leader of this latter organization (which was founded in 1891 by Katherine Brandegee) from 1950 to 1970. Over the years he was a mentor to a loyal following of amateur and professional botanists. Tom's influence extended beyond informal botanical instruction and encouragement. In many cases he nurtured dedication among his followers that led to important collaborative publications such as *A Flora of San Francisco* (1958), *A Flora of Lassen Volcanic National Park, California* (1961), *The Vascular Plants of Monterey County, California* (1964), and "A Catalogue of Vascular Plants on Peavine Mountain" (1992). In the years preceding his death Tom was actively involved in a collaborative study of the flora of Sonoma County. Tom was especially proud of having received the Willdenow Medal from the Berlin Botanical Garden and Museum (1979) and the Fellows Medal of the California Academy of Sciences (1986). Following his retirement, the John Thomas Howell Curatorial Chair of Western American

Botany was established at the Academy. The endowment for this chair continues to grow and it will be activated when sufficient funds become available. His many friends and colleagues will miss Tom's thoughtful counsel, ever present humor, and zest for the flora of his native state. A biographical sketch of Tom Howell's eventful and productive life appeared in *Fremontia* 17:11–19, 1989. A memorial service for Tom was held at the Academy on 8 July 1994.

—THOMAS F. DANIEL, FRANK ALMEDA, and DENNIS E. BREEDLOVE, Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, USA.

HERBERT L. MASON
1896–1994

Herbert Louis (né Lewis) Mason, Professor Emeritus of Botany, University of California at Berkeley, died peacefully in Bellingham, Washington, on March 26 at the age of 98. He served as editor of Madroño from 1935 to 1963, with the indispensable assistance of Ethel Crum, Helen Sharsmith, and, most importantly, Annetta Carter, transforming it from an almost parochial publication into an important botanical journal. From 1941 to 1963 he was Professor of Botany and Director of the University Herbarium (UC).

Mason was born in Fond du Lac, Wisconsin, on January 3, 1896, one of a pair of identical twins who were the eighth and ninth children of Thomas and Harriet Mason. His interest in botany developed as a child, influenced by his mother's love of gardening and her informal teaching of botany to Herbert and his twin Walter (who ultimately became a florist). The twins entered Stanford University from high school, but volunteered for military service in World War I. They were trained as cooks in Georgia and stationed at an army hospital in Beaune, France. From this experience, Herbert attained proficiency as a cook, a life-long love of opera, and considerable respect for things French.

Returning to Stanford after the war, Herbert received an A.B. in 1921, crediting LeRoy Abrams with kindling his interest in plant taxonomy. He obtained an M.A. from the University of California at Berkeley in 1923, and then taught during 1923–1925 at Mills College, an institution for which he retained a life-long affection. During summers he worked for the Carnegie Institution of Washington, first assisting in F. E. Clements' altitudinal transplanting program in Colorado, and later hunting for plant fossils with R. W. Chaney in the John Day formation of central Oregon. Mason joined the Department of Botany at Berkeley in 1925 as an Associate in what W. L. Jepson referred to as the Phenogamic Laboratory. In 1931 he married fellow Stanford graduate and Berkeley graduate student Lucile Roush, a student of coralline algae working with W. A. Setchell. Immediately after the wedding, he departed for Alaska, where, for the Carnegie Institution, he collected taxodiaceous fossils on St. Lawrence Island in Bering Strait. Both Herbert and Lucile were awarded the Ph.D. in 1932. His thesis dealt with western American Tertuary paleobotany, and was administered by a committee comprising W. L. Jepson (chairman), R. W. Chaney, and C. L. Camp.

The 20's and 30's were an era of intensive efforts to incorporate into biological taxonomy and ecology not only the consequences of Darwinian evolution, but also the more recent findings of genetics and particularly cytogenetics. Mason was strongly influenced by and became a major participant in the group of Bay Area biologists and earth scientists who engaged in the interdisciplinary discussions and activities that led to the formation of a still-active group called The Biosystematists and to the rise of Biosystematics itself. He wrote in 1950: "I have grown up along-side of Biosystematics and have shared the enthusiasm of its workers, and am aware of its values, and know something of its limitations." Blessed with curiosity and an open,

receptive attitude, Mason was willing to consider evidence of every kind to solve problems of classification and distribution-growth hormones, population genetics, polar migration, continental drift. However, his paleontological experience made him sensitive to the fragility of rigid categories and he was skeptical of hierarchical units in both taxonomy and ecology. "The species of Linnaeus vary all the way from separate genera to synonyms of one another—there is no 'Linnean species' as such. The same applies to everyone else's concept of taxonomic units." He was particularly critical of the Clementsian school of plant ecology, which attributed quasi-organismal qualities to "associations," "climaxes," and other phytosociological abstractions.

Mason's interests ranged widely, and his long editorship of Madroño enabled him to employ its pages to comment incisively and frequently on a broad range of topics. A series of papers in the 1930's dealt with the fossil occurrences of the so-called closed-cone pines, and their bearing on the geological history of California islands and coastline as well as on conifer phylogeny. His specifically taxonomic studies concentrated on *Dodecatheon* in the 1930's and later shifted to Polemoniaceae, where he emphasized the striking diversity of floral architecture. He employed Alva Day Grant as an artist and trained her so thoroughly in this complexity that she shared with him authorship of his major exposition of this family in Abrams' *Illustrated Flora of the Pacific States* (1951). The California Division of Fish and Game initiated discussions in 1945 toward undertaking a botanical survey of the state's wetlands. This enterprise, which involved the field activities of Verne Grant, Malcolm Nobs, and S. Galen Smith, culminated in the production of *A Flora of the Marshes of California* (1957), embellished by the superb line-drawings of Mary Barnas Pomeroy, in what is doubtless his best-known work.

His emphasis turned increasingly toward understanding the underlying causes of the distribution and evolution of plants in time and space, a discipline he termed "plant geography" to distinguish it from Clementsian plant ecology. He viewed plant geography as a dynamic rather than a purely static, descriptive discipline.

His classic paper, "The edaphic factor in narrow endemism" (1946), was among his most influential. Mason brought to plant geography physiological, evolutionary, and taxonomic components. He was constantly revising his lecture notes for the two courses he usually taught—Plant Geography and Phylogenetic Taxonomy, and many of his published papers sprang from this source. His influence on the organization and content of Stanley Cain's landmark book *Foundations of Plant Geography* (1944) was considerable and perhaps less adequately acknowledged than it might have been. R. H. Whittaker also profited substantially from Mason's ecological insights. In spring, 1951, Mason spent a sabbatical leave at the University of Nebraska, searching for more evidence on the evolutionary views of Charles E. Bessey. This work was also related to a plan to write a "quite novel" taxonomy text with his former student J. A. Davidson. The emphasis of the text was to be "the development of taxonomy as a philosophy of science" and, although a completed first draft over 500 pages long was announced in 1952, it failed to be published.

Throughout his career, but more prominently in his later years, Mason was interested in several theoretical and philosophical issues. These were reflected by a thoughtful and now-ignored clarification and discussion of the terms taxonomy, systematic botany, and biosystematics (1950), in which he makes a clear distinction between the gathering of facts (systematic botany), their application in a taxonomic framework (taxonomy), and a particular, and then rather new, methodology (biosystematics).

Mason became strongly preoccupied with his analyses of various biological problems, aired them almost without invitation, and was quick to exhibit impatience with colleagues who either failed to understand his arguments, or worse, to appreciate their significance. Ecologist Jean Langenheim, then resident in Berkeley, became a close associate of Mason during the 1950's, and was instrumental in helping him translate his often abstruse ideas into more readily understandable language. His 1957 paper, "The concept of the flower and the theory of homology" devoted much attention to Zimmermann's then fashionable "telome theory" and its role in under-

mining confidence in "our concepts of the flower." In the same year Mason and Langenheim published their joint "Language analysis and the concept environment," and in 1961 their "Natural selection as an ecological concept" appeared. The first paper argued that the concept of environment is significant only in that environmental features reflect "some aspect of the operational relations of the phenomena to organisms." We cannot determine the degree to which either paper has impacted evolutionary or ecological thought, but even today both of them are refreshing to read whether the reader agrees with the arguments or not.

To those of us who knew Herbert Mason as a colleague (Constance) or as his student (Ornduff), his influence on our thinking is strong if not always conscious or acknowledged. Langenheim (personal communication) acknowledges Mason's unique way of intellectually probing ideas, and his remarkable foresight in identifying significant ecological issues. Mason's student Arthur Kruckeberg has written to us: "While Herbert eschewed the main-stream of American ecology in the 1940's and 1950's, he was in fact engaged in ecological thinking. He espoused a Gleasonian approach to plants and their environments. Simply put, he believed that single species or populations matched their environments . . . by virtue of genetically controlled spans of physiological tolerance . . . This spartan, individualistic approach to plant ecology took on a special meaning for Mason, particularly as he viewed the rich endemism of the California flora. Mason's illumination of edaphic causes of endemism provoked a flurry of research soon after the 1946 papers appeared. Hans Jenny, James Vlamis and Richard B. Walker probed the physiological basis of serpentine tolerance, while Arthur Kruckeberg and Calvin McMillan took on the issue of the genecological basis of the plant response to serpentine soils. The linkage between narrow endemism and unusual edaphic conditions was forged by Mason and it has proved a heuristic model ever since."

In the 1950's Mason became very much interested in and preoccupied by mathematical set theory as it relates to the organization of taxonomic knowledge. This new-found interest came to dominate the lectures in his two-semester course on Phylogenetic Taxonomy, but so far as we know, he never published any of his ideas in this area. Nevertheless, Mason's ideas about plant systematics and his approach to the field, while perhaps not formally acknowledged, have had a strong impact. Peter Raven has written to us that "Herbert Mason was the best university teacher whom I encountered during my undergraduate education. Consistently stressing access to original literature, and a method of inquiry and analysis, he led many of us to understand a great deal, not only about the characteristics of plants that were of significance in interpreting their phylogeny, but also and especially about the philosophies that underlaid the intelligent use of those characteristics . . . his influence on successive classes of Berkeley students has made a very real impact on the development of the field of systematic and evolutionary botany that will be felt for years to come."

Despite a certain formal manner in classroom situations, Mason was an excellent informal speaker, very popular with garden clubs and other groups, and a resourceful story-teller, full of anecdotes about the many biologists he knew. He obviously enjoyed teaching and his contact with students and laymen. For many years he was active in the Yosemite Field School for the training of naturalists. He initiated a field course in taxonomy that was given in the summers of 1957 and 1958 at Berkeley's Sagehen Creek field station north of Truckee. Shortly before his retirement he became one of three founders of the Elementary School Science Project, funded by the National Science Foundation and operated out of the Lawrence Hall of Science. This project aimed at enhancing the science expertise of students in California grade schools. After he retired, Mason was recalled to service as director of this project, one which has had a continuing and important impact on science education in the United States. These activities came at the close of Mason's academic life but, according to former Lawrence Hall of Science Director W. M. Laetsch, Mason reflected on his role in that project as the most interesting and important thing he had done in his career.

It was a remarkably full and varied career. Both Herbert and Lucile Mason were continuously involved with students, colleagues, and long-time friends. They were famous for their hospitality. Shortly after Herbert's retirement in 1963, they moved to Bellingham, Washington, to be near their son David, who is a professor at Fairhaven College of Western Washington University. David devoted himself unstintingly to his parents' welfare. Lucile died in 1986. The sixteenth volume of Madroño is devoted to Herbert, with an excellent Marion Cave photograph of him as we like to remember him. — ROBERT ORNDUFF and LINCOLN CONSTANCE, University and Jepson Herbaria, University of California, Berkeley 94720.

ANNOUNCEMENT

DR. LYMAN BENSON BOTANY RESEARCH LIBRARY
DONATED TO DESERT BOTANICAL GARDEN

The library collection of one of the most prominent botanists of the Southwest during the past century, Dr. Lyman Benson, was recently donated to the Desert Botanical Garden in Phoenix, according to Dr. Robert Breunig, the Garden's executive director.

"The Desert Botanical Garden has one of the finest desert plant collections in the world," said Dr. Breunig. "Dr. Benson's life-long plant research contributed immeasurably to our knowledge of desert plants." He added that it is fitting that this great plant collection and the library of this great scientist be joined through this generous gift. Both collections will continue to be invaluable to the ongoing study of desert plants of Arizona and the Southwestern United States.

Dr. Benson, who died in 1993, is well known as the author of *The Cacti of the United States and Canada* and *The Native Cacti of California* published by Stanford University Press. He also co-authored, with Robert A. Darrow, *Trees and Shrubs of the Southwestern Deserts* and authored *The Cacti of Arizona* published by the University of Arizona Press.

The donation of the collection resulted from the long association of Dr. Benson with his former student Dr. Edward Anderson, the Garden's senior research botanist. Dr. Anderson studied botany with Dr. Benson, who was chairman of the Botany Department at Pomona College in Claremont, CA. Dr. Benson also taught, from 1938 to 1944, at the University of Arizona, Tucson.

The collection will be housed in the Garden's research library and made accessible for research use by appointment.

The Desert Botanical Garden, located in Papago Park at 1201 N. Galvin Parkway in Phoenix, is open from 7 a.m. to 10 p.m. daily. Admission is $5 for adults; $4 for seniors; $1 for children 5–12; and free to children under 5. For more information about the Benson collection contact the Garden's librarian Jane Cole at 941-1225.

REVIEWS

California's Changing Landscapes. By Michael Barbour, Bruce Pavlik, Frank Drysdale, and Susan Lindstrom. 1993. California Native Plant Society. 244 pages. Softcover $24.95. ISBN 0-943460-17-4.

California's floristic diversity, composed of approximately 5000 native species and slightly over 1000 naturalized alien species, is organized into a remarkable assemblage of distinct to intergrading plant communities. Their collective ecological diversity is unparalleled in equivalent areas on the North American continent. Although much current interest is focused statewide on the abundance and threats to individual taxa, relatively less attention has been given to California's plant communities, higher order vegetation types or formations, and ecosystems. The authors have correctly drawn attention to these components of California's floristic diversity and the complex physiographic factors affecting its distribution and physiognomy. They have done so with eloquence and with an economy of words.

The text is divided into 8 chapters, of which the first introduces the concept of landscape as influenced by change over space and time. Geochronological events, fire, human interference, and interactions among regional topography, geological substrates, and climate are each introduced as major environmental determinants. The 5 following chapters, with eye-catching titles unencumbered by traditional phytosociological terms, are organized sequentially to give a longitudinal perspective of California's vegetation. This sequence begins with the immediate coast and continues eastward to include the coastal forests, the Central Valley, the Cascades and Sierra Nevada, and the eastern deserts. Although these physiographic regions are indeed predominant features of California's landscape, I found it disconcerting that the continuum of woodland and forest between the Klamath and Cascade Ranges was neglected. Also neglected was the southern fourth of California, where a central valley is lacking and the only major topographic barriers between the coast and desert are the Transverse and Peninsular Ranges.

Each of the 5 chapters devoted to major ecosystems reiterates themes of uniqueness, diversity, and change, enhanced by brief essays on the biology of selected species and their adaptation(s) to habitats characteristic or special to the chapter's topic. Most of these vignettes tantalize the reader with exciting examples of plant biology. Chapters on the coastal forests and California's high mountains offer succinct accounts of major forest communities and highlight the ecological factors that influence establishment of seedlings and the relative distribution of different species. Sadly, the authors did not emphasize the remarkable diversity of conifers, unsurpassed elsewhere in North America, that occurs in California's montane forests, especially in the Klamath Range. I found the chapter on California's Central Valley equable in the treatment of formerly widespread vegetational landscapes and their ecology. The discussions of much diminished riparian forests, tule marshes, grasslands, and foothill woodland in this chapter were particularly interesting from a historical view and provided a glimpse of what the pre-Spanish, Great Valley may have been like. On the other hand, the chapter on California's 3 major deserts, which comprise nearly 30% of the state's land area, did not seem to treat adequately what may well be the state's largest remaining assemblage of pristine plant associations.

The penultimate chapter, which summarizes the relationship between native Californians and the vegetational landscape, is not a traditional topic of plant and landscape ecology. However, it provides an illuminating perspective on the contrast between a 12,000 year history of pre-Spanish human presence and the seemingly

catastrophic interference and exploitation of the most recent 200 years. Much of its contents are devoted to specific examples of native plants important to the hunting-gathering culture of California's diverse native cultures. The extensive use of fire by native Americans, in the intelligent management of vegetation for sustenance, is given appropriate attention and should engender important ecological questions concerning the extent, structure, and recent geobotanical history of several natural plant community types.

The final chapter, which provides 3 scenarios to the restoration of vegetation, discusses issues of concern to all Californians. Each scenario provides a glimpse of the potential for and challenges to ecological restoration. Several apparently successful examples are discussed in the attempt to show what can be achieved with determination and cooperation among diverse interests. However, a few of these examples, in my opinion, may well represent efforts at reconstruction rather than restoration. The example of Santa Cruz Island needs clarification. The discussion makes no mention of failed attempts to remove feral pigs, whose activities probably contribute much to an apparently historical decline in bulbous taxa, the failure of oak regeneration from seed, and local substrate disturbance. Furthermore, the restriction of sheep to fenced pastures has not been successfully accomplished.

Although the book provides a broad view of natural history, some discussions or statements were too superficial and did not adequately convey the complexity of specific biological patterns. A few statements contained errors. I was dismayed to read (p. 36–37) that Big Sur is implicitly treated as a discrete boundary between evergreen-dominated northern coastal scrub and drought-deciduous southern coastal scrub. I would have preferred a discussion that emphasized the apparently patchy transition between these community types, a transition that actually extends as far south as western Santa Barbara County. I can't accept the Mojave Desert as an ecotone (p. 139) between the Great Basin and Colorado Deserts. Most phytogeographers consider it a floristic province, with its own endemic taxa and such unique communities as Joshua Tree woodland. Referring to *Sarcodes* as a parasite (p. 102) is incorrect and inconsistent with the definition of a parasite in the glossary. *Sarcodes* does not consume its host but rather derives its nutrition from conifers via a fungal intermediate. That Jeffrey and Ponderosa Pines "meet, mingle and miscegenate" (p. 112) seems a nicely executed alliteration. Unfortunately "miscegenate" has anthropomorphic and pejorative connotations and is not an appropriate synonym for the widely accepted and widely understood term "hybridize". The correct varietal name for Sierran white fir (p. 126) is var. *lowiana*. The leaves of cacti (p. 143) have not been "eliminated" during evolution, as the authors imply; rather they have been modified into glochids and spines. I was especially disappointed in the admittedly speculative treatment of grassland, a controversial subject of special interest to current restoration ecology. Although California botanists traditionally favor species of *Nassella* (formerly *Stipa*) as likely dominants, I found no meaningful biological explanation for this conclusion nor did I read why other common native species, including *Poa secunda, Muhlenbergia rigens,* and *Hordeum brachyantherum,* are rarely if at all considered. Much of the discussion centered on the pros and cons of grazing, first by native animals and later by feral animals. However, literature on food habits of both native elk and antelope, which comprised the grazing herds of Holocene California, suggests that grasses were a relatively minor dietary component. Interactions among several other ecologically important factors, including seasonal precipitation, fire, and competition for water determine the distribution of grasslands elsewhere in North America, but the same in California grasslands were not addressed.

These shortcomings detract somewhat from a book that otherwise lucidly conveys and summarizes the extensive scientific knowledge gained from many decades of study. The text is richly illustrated and the photographs are well chosen. Although the color plates are excellent, a number of black and white photographs are poorly reproduced. The text is complemented by a list of pertinent references and suggestions for further reading, an informative, carefully written glossary, and an index with cross-references to scientific names. The overall content and style reflect the collective

knowledge, experience, and skills of the several authors, each with different backgrounds and interests. Professional botanists need to read it as an example of what can be done to extend scientific knowledge and its applicability to general education and conservation efforts. Although not especially useful as a primary reference, this book represents an exceptional contribution by its authors and the California Native Plant Society to fostering interest, concern, and a continuing appreciation for the natural landscapes of California.

—DIETER H. WILKEN, Santa Barbara Botanic Garden, 1212 Mission Canyon Rd., Santa Barbara, CA 93105.

Practical Handbook for Wetland Identification and Delineation. By J. G. LYON. 1993. Lewis Publishers, Boca Raton. 157 pages. Hardcover $59.95. ISBN 0-87371590X.

This "practical handbook" is anything but practical, and attempting to follow its guidance will likely do more harm than good. Wetland delineation is a critical decision-making process that requires well-trained experts. This book is elementary in its language and approach, seeming to interpret the complexities of delineation for a lay audience, yet its intent is clearly to teach readers how to develop wetland delineation reports. It does not achieve either objective.

In addition to the awkward writing, repetitive wording, redundant statements, and grammatical errors (e.g., "From it stems the three criterion . . ."—p. 11) that litter virtually every page, the content is imprecise, misleading, and in many cases just plain wrong. I quote first from the section on plant measurements, which tells us how to record information on vegetation (p. 67): "The scientific names have two parts written in Latin. The first word is the family or generic name. . . . The second name is that of the individual plant or plant species in the family."

More importantly, the criterion for hydrophytic vegetation is repeatedly misstated: "A given site is determined to be a wetland for this criterion when the total dominance of FAC, FACW, and OBL plants exceeds 50% of the total dominant plants found on the site"—p. 26; "The procedure consists of determining whether 50% of the dominant plants have a high probability of occurring in wetlands"—p. 42; and "A given area is determined to be a wetland for this individual, jurisdictional criterion when the total abundance of FAC, FACW, and OBL plants exceeds 50% of the total frequency of dominant plants found at a given sampling location on the site"—p. 67. None of these renditions makes it clear that one must count the number of dominant species to determine if more than 50 percent are OBL, FACW, or FAC, and none of Lyons' advice correctly states that this is only ONE of the acceptable ways of meeting the vegetation criterion (see 1987 Federal Manual, p. 19).

The level of advice is highly variable. On page 37, a paragraph is devoted to pacing a 100-foot line—a simple task, yet a much more difficult procedure is not elaborated: "Record whether sample points have similar or dissimilar soils to those indicated by the county Soil Survey." Such decisions require technical knowledge and experience. Likewise, without much help, readers are instructed to sample sites at 100-foot intervals and then "supply the boundaries of any jurisdictional wetlands"—p. 44. The inclusion of numerous photographs (47 full pages or 30% of the book) might appeal to a general audience, but the captions use technical terms that are not defined, and they sometimes promise more than pictures can deliver (figure 2.3 on p. 10 is an inundated wetland, for which hydric soils are supposedly "evident").

My comments are lengthy, but it seemed necessary to document carefully this negative review. I cannot recommend the book for any audience. I suggest instead that prospective wetland delineators study the appropriate federal manual (currently the 1987 Wetlands Delineation Manual available from the US Army Corps of Engineers, Washington, D.C. 20314-1000).

—JOY B. ZEDLER, Pacific Estuarine Research Laboratory, San Diego State University, San Diego, CA 92182-0057.

This guide presents "a systematic and descriptive enumeration of the grasses of the Lower Rio Grande Valley (LRGV), Texas." As such, it treats 183 grass species, including eight endemics, of the plains, prairies, and marshes of the four southernmost Texas counties, Starr, Hidalgo, Willacy, and Cameron. The treatment is in traditional format (though perhaps not in traditional order): introduction, keys to genera, taxonomy of the genera and species, literature cited, index, glossary, and illustrations.

The focus of the guide is on identification. The Introduction contains a discussion of the structure and arrangement of grass parts, supplemented by illustrations. Descriptions of genera and species are unusually complete and detailed for this type of field guide. Over half (101) of the species are illustrated. The identification keys are flush left, with the two corresponding leads together. This saves space, but prevents the visual clustering of similar species so easily done with indented (or yolked) keys. The keys require an early examination of tiny spikelet parts—identification of *Bothriochloa* demands that the user distinguish at the third and fourth choices the differences among dioecious, bisexual, and reduced florets. I would have hoped for a more layman-oriented approach, using where possible features external to the spikelets, in this case disarticulation, size and texture of glumes, compression, and arrangement of sessile and pedicelled spikelets. For this reason, the guide will serve very well as a lab aid to grass identification in college courses where dissecting scopes and lab instructors are handy. It will be of less benefit to ranchers, naturalists, range managers, and other laymen, though still usable. Perhaps because of the emphasis on identification, the little tidbits and trifles about grasses that intrigue and tantalize us are mostly lacking. The blood-letting blades of *Leersia*, use of *Arundo* for woodwind reeds, the toxicity of *Eragrostis cilianensis*, hidden cleistogamous spikelets of *Leptochloa dubia*, these are the details that we taxonomists often leave out of floras and field guides, but that we most desperately need to include if we are ever going to make our science accessible and interesting to the public. The brief discussion of the four major habitats in the LRGV with their characteristic grasses is an excellent addition in this regard. A little natural history goes a long way.

The most eye-catching feature of this guide is the illustrations. Grouped at the back of the book rather than near the species in question (perhaps only an annoyance), the species are rendered in an unusual reverse white on black format. Seemingly drawn from herbarium specimens, they capture the salient features of the grasses well, though sometimes not in close detail because of size constraints. Unfortunately, some are lacking in contrast and one can't help but squint to try to make the images stand out, but overall, the illustrations will be an excellent aid in identification.

Typographical errors seem to be few and minor. The size (13.5 × 21 cm) is perfect for a field guide and encourages one to stuff it into a daypack on field trips. Deliberate attempts to crack or weaken the binding failed; the pages remained bound.

We need more regional and local field guides like this one. The current emphasis on large-scale, multi-authored floristic treatments (e.g., Flora of the Great Plains, Flora of North America, The Jepson Manual) should never be allowed to undermine the importance of local contributions from the grassroots botanical community.

—KELLY W. ALLRED, Department of Animal and Range Sciences, New Mexico State University, Las Cruces, NM 88003.

Subscriptions—Membership

Membership in the California Botanical Society is open to individuals ($22 per year; students $12 per year for a maximum of seven years). Members of the Society receive Madroño free. Family memberships ($25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to Madroño are available ($50). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of Madroño should be sent to the Corresponding Secretary.

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Contents

A REVIEW OF *CRYPTANTHA FULVOCANESCENS* (BORAGINACEAE) AND RE-EVALUATION OF GREENE'S *OREOCARYA NITIDA*

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ABSTRACT

Cryptantha fulvocanescens has a long history of confused taxonomic treatment, exacerbated primarily by the persistent misinterpretation of *Cryptantha echinoides*. *Oreocarya nitida* was mistakenly submerged into synonymy of *C. fulvocanescens* in 1927. It has remained in obscurity because of the many confusing treatments of this variable and difficult group of taxa. *Cryptantha fulvocanescens* var. *nitida* is a new combination for a taxon endemic to the upper Colorado River Basin. It is distinguished from var. *fulvocanescens* most notably by the dense silvery pubescence on the inner surfaces of its calyx lobes.

REVIEW

In 1901, Greene published the name *Oreocarya nitida* with the description of a plant collected by C. F. Baker (*No. 95*) from Deer Run, Colorado. The epithet *nitida* refers to the "bright" silver or canescent hairs on both surfaces of the calyx lobes. Macbride (1916a) recognized *O. nitida* Greene in his revision of the genus but had a poor understanding of its delimiting characteristics. By relying entirely on plant height and color, he placed three of the six almost identical specimens of *O. nitida* he examined within *Oreocarya fulvocanescens* (S. Watson) Greene. Macbride's uncertainty was expressed in his postscript, "Possibly this plant is only a large variety of *O. fulvocanescens.*" That comment and Macbride's confused jumble of specimen citations led Payson (1927) to consider the two taxa synonymous when he transferred the members of *Oreocarya* to *Cryptantha*. Unfortunately, Payson placed particular emphasis on the materials previously identified as *O. nitida* in the formulation of his concept of *Cryptantha fulvocanescens* (S. Watson) Payson.

To separate successfully Greene's *nitida* concept from other historical treatments, it is necessary to give a complete taxonomic review of *Cryptantha fulvocanescens*. The first publication of the name was by Watson (1871) in reference to Nevada (and possibly Utah) materials collected by Fremont and a Fendler collection from

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New Mexico that he named *Eritrichium glomeratum* A. de Condolle var. (?)*fulvocanescens*. Watson had seen the name *E. fulvocanescens* as used by Gray to label the Santa Fe, NM, collection by Fendler (*No. 632*). He accepted that specimen as one of his new variety and used the epithet *fulvocanescens* in his trinomial. Watson, however, was not successful in separating distinct species because he included Fendler's New Mexico collection with Fremont's Nevada specimens, which are, in part, conspecific with the type of *Cryptantha humilis* (A. Gray) Payson (Johnston 1932). Watson's aggregate taxon later caused confusion in determining which entity should be associated with the name *fulvocanescens*.

When Gray (1875) finally published *Eritrichium fulvocanescens*, based upon Fendler's New Mexico collection, he was forced to accept Watson's trinomial as a synonym because Watson had referred to the Fendler collection in its publication. For many years this clouded the identity of a type specimen and locality because Watson's original description also included Fremont's Nevada collections. The New Mexico type locality gained acceptance when Macbride (1916b) supported Gray's concept of *fulvocanescens* and Payson (1927) cited the *Fendler 632* collection as the type for *fulvocanescens*. Johnston (1932) was most succinct in his summation: "since Watson included the Fendlerian New Mexican plant in his concept and indicated it was the source of his name, then, it should be taken as the type of *fulvocanescens*, both as variety and species."

In the interval between Gray's (1875) and Macbride's (1916b) publications, the name *Krinitzkia echinoides* M. E. Jones was published for two Utah collections and Fendler's New Mexico collection (Jones 1895). The epithet *echinoides* refers to the minute, bristly setae that ornament the nutlet murications on most *fulvocanescens* to some greater or lesser degree (see Cronquist et al. 1984 for illustration). Jones recognized these plants as different from those of Watson's concept of *fulvocanescens* and determined Fremont's Nevada collections to be "a low altitude variation of *K. sericea* (Gray) i.e., var. FULVOCANESCENS." He included the Fendler collection of Gray's *fulvocanescens* concept in his new species by stating, "the original *Eritrichium fulvocanescens* of Gray . . . based on Fendler's collection from New Mexico is *K. echinoides,* though the specimen is only in flower." Had he inspected the more mature duplicates of Fendler's collection he would have found numerous setae ornamenting the nutlets. In fact, Gray's *fulvocanescens* description of "nuculis granulato-scabris" undoubtedly referred to this characteristic. *Krinitzkia echinoides* is, therefore, a superfluous and illegitimate name. The name *echinoides* should not have continued to be used. It did persist, however, and later became the confounding element between Gray's *fulvocanescens* and Greene's *nitida* concepts.

While monographing this group, under the genus name *Oreocarya,* Macbride (1916a) was faced with its complex synonymy. He disagreed with Jones's inclusion of Fendler's New Mexico collection in *echinoides* and correctly maintained it as the legitimate *fulvocanescens.* Macbride (1916b) further stated "it is rather the plant collected by Watson (actually Fremont's Nevada collections) and wrongly included by him in his description of *fulvocanescens* as a variety of *glomerata* which needs the new name. . . ." He then mistakenly applied the name *Oreocarya echinoides* Macbride to *Eritrichium glomeratum* var. *humile* Gray as having species level priority over Greene's (1896) publication of *Oreocarya humilis* (A. Gray) Greene. Although Macbride retained Jones as the parenthetical authority of *O. echinoides,* Macbride's is the first legitimate publication of name *echinoides* and it referred to a distinctly different concept. *Oreocarya echinoides* Macbride is, therefore, a synonym of *Cryptantha humilis* (A. Gray) Payson.

The next appearance of the name *echinoides* occurred in Payson's (1927) monograph. Payson resurrected Jones's illegitimate name as *Cryptantha echinoides* Payson and cited three specimens that have dense setae on the nutlets. He acknowledged, but purposely disregarded, Jones's statement that Fendler's New Mexico collection is *echinoides* and designated Jones's *5297p* "with hedgehog-like nutlets" as the type for his *C. echinoides.* By retaining *echinoides,* Payson was faced with the problem of finding an identity for *fulvocanescens.* He accomplished this by submerging *O. nitida* into synonymy with *Cryptantha fulvocanescens.* Because *nitida* plants have few, if any, nutlet setae, this combination of taxa gave him the necessary diagnostic criterion to separate *echinoides* from his new concept of *fulvocanescens.* Therefore, Payson's description and most of his specimens cited for *C. fulvocanescens* are actually conspecific with the type of Greene's *nitida,* while his description and specimens cited for *C. echinoides* fit comfortably into Gray's *fulvocanescens.*

While preparing for a revision of the perennial species of *Cryptantha* (subg. *Oreocarya*), Higgins (1969) used the name *echinoides* (again attributed to Jones, with lectotypification attributed to Payson) in a trinomial with *C. fulvocanescens.* After a brief sojourn as the variety *C. fulvocanescens* var. *echinoides* [M. E. Jones] L. C. Higgins (1969), the name *echinoides* was placed into synonymy with *C. fulvocanescens* (Cronquist et al. 1984). This left one highly polymorphic taxon, which tends to minimize the compelling variability that led to much of the confusion described above. In addition to nutlet characteristics, this variability includes the indument variation that originally inspired Greene to describe *O. nitida.*

Oreocarya nitida was resurrected by Weber in his Colorado Flora: Western Slope (1987). Unfortunately, that regionally delimited flora does not allow for diagnostic distinction of *nitida* from *fulvocanes-*

cens. While it is gratifying to see *O. nitida* back in use, two problems may forestall its general acceptance by contemporary botanists. The first is the maintenance of *Oreocarya* as a distinct genus. *Cryptantha* and *Oreocarya* are differentiated only by, respectively, annual and perennial habits. Johnston (1924) studied the distinguishing attributes of both genera and questioned whether they should remain distinct or be combined as *Cryptantha.* The combination of the two genera was accomplished by Payson (1927) in his monograph of the perennial species as *Cryptantha* sect. *Oreocarya* and reinforced by Higgins's (1971) revision of *Cryptantha* subg. *Oreocarya.* The second problem is recognition of *nitida* as a species. Many salient characteristics of *fulvocanescens* and *nitida* are very similar. Their distinctive, but minor, differences appear to result from geographic sorting of variations that occasionally overlap in the few areas of sympatry. Therefore, *nitida* is more suitably recognized at an infraspecific level within *Cryptantha fulvocanescens.*

Taxonomic Treatment

Key to the Varieties of *Cryptantha fulvocanescens*

A Calyces densely hispid-strigose; interior faces of calyx lobes strigulose, the green
   surfaces partly visible .... 1a. var. *fulvocanescens*
A' Calyces densely strigose and sparsely hispid; interior faces of calyx lobes densely
   silvery strigose, the green surfaces obscured .... 1b. var. *nitida*

1. **Cryptantha fulvocanescens** (S. Watson) Payson, Annals of the Missouri Botanical Garden 14:319–321. 1927.—*Eritrichium glomeratum* A. de Condolle var. (?)*fulvocanescens* S. Watson, Botany *in* C. King, Report of the Geological Exploration of the Fortieth Parallel 5:243. 1871.—*Eritrichium fulvocanescens* (S. Watson) A Gray, Proceedings of the American Academy of Arts and Sciences 10:61. 1875.—*Krinitzkia fulvocanescens* (S. Watson) A. Gray, Proceedings of the American Academy of Arts and Sciences 20:280. 1885.—*Oreocarya fulvocanescens* (S. Watson) Greene, Pittonia 1:58. 1887. Type: USA, New Mexico, Santa Fe Co., "Declivities of dry, gravelly hills southwest of Santa Fe," 1847, *A. Fendler 632* (lectotype: GH!—Higgins, Great Basin Naturalist 28:42. 1971; isolectotypes: GH!, PH, US).

Caespitose perennials from woody branching caudices. Stems several from persistent mat of basal leaves, erect, 5–30 cm tall, strigose and hispid. Leaves oblanceolate to spatulate, acute or obtuse, 15–70 mm long, 3–10 mm wide, densely and uniformly coarse-strigose, pustules obvious only on abaxial surfaces of previous year's leaves. Inflorescences, helicoid arrangements of cymes that appear as short,

unilateral, false spikes, narrow or somewhat open at maturity, rarely subcapitate. Cymes 2–11-flowered. Distal foliar bracts reduced, marginally hispid. Bractlets usually present, 1–2 mm long. Pedicels 1–8 mm long. Calyces 4–9 mm long at anthesis, 6–13 mm long in fruit, lobes linear, hispid-strigose. Corollas white to ochroleucous, tubes 7–13 mm long, exceeding calyx lobes by 2–5 mm, crests at bases of tubes usually lacking, fornices yellow and rounded or shallowly emarginate, limbs 6–9 mm broad, rotate, often reflexed after anthesis. Styles heteromorphic, exceeding mature fruits by 2–7.5 mm. Nutlets lance-ovate, 3.1–4.4 mm long, 2–3 mm wide, usually 1, sometimes 2, maturing, margins acute, in contact when more than 1 nutlet present, both surfaces muricate, often with sharp, setose tips terminating some or all murications, scars closed or only slightly open.

1a. CRYPTANTHA FULVOCANESCENS (S. Watson) Payson var. FULVOCANESCENS. *Krinitzkia echinoides* M. E. Jones, Proceedings of the California Academy of Science II. 5:709–710. 1895, nom. superfl. illegit.—*Cryptantha echinoides* Payson, Annals of the Missouri Botanical Garden 14:321–323. 1927.—*Cryptantha fulvocanescens* (S. Watson) Payson var. *echinoides* (Payson) L. C. Higgins, Great Basin Naturalist 28:30. 1969. TYPE: USA, Utah, Kane Co., Pahria Canyon, 26 May 1894, *M. E. Jones 5297p* (lectotype: POM!—Payson, Annals of the Missouri Botanical Garden 14:322. 1927).

Indument fulvous or white. Cymes 2–7-flowered, loosely scorpioid, internodes often reduced so flowers appear in pairs. Fruiting pedicels 3–8 mm long. Calyx lobes densely hispid-strigose on abaxial surfaces, thinly strigulose on adaxial surfaces. Nutlet surfaces muricate and usually with short, sharp setose projections terminating many murications at least on nutlet margins or abaxial surfaces. $n=12$ (Sivinski 1993).

This is a highly variable taxon. The indument is typically fulvous; some scattered populations in northern and southern New Mexico have white indument. The variation in indument color is neither regionally consistent or habitat specific. Some plants have a dense coverage of setose tips on the nutlet murications while others have few or no nutlet setae. The presence/absence or relative density of nutlet setae does not correlate consistently with geographic distribution and can vary considerably among plants within a population. Although there is no holotype for this species, Higgins (1971) designated a *Fendler 632* specimen at GH as the holotype and, thereby, effected lectotypification.

Distribution. Central and southern Utah, Arizona north of the Mogollon Rim, to north and south-central New Mexico (Fig. 1). On shaley, gypseous, or caliche sands in piñon-juniper woodland, Great Basin Desert scrub, and Chihuahuan Desert scrub at elevations from 1200 to 2300 meters.

Representative specimens. USA, ARIZONA: Apache Co., 24–27 km N. of Ganado, 10 Jun 1937, *Peebles 13479, 13490* (GH); Navajo Co., 1.6 km S. of Taylor, 18 May 1970, *Atwood 2580* (BRY); near Winslow, 20 May 1934, *McKelvey 4537* (GH). NEW MEXICO: Catron Co., Tejana Mesa, 8 km NW of Quemado, 7 Jun 1991, *Sivinski 1710* (UNM); Otero Co., White Sands National Monument, 4 May 1933, *Castetter 2127* (RM, UNM); Santa Fe Co., hills at Santa Fe, 13 May 1897, *Heller 3517* (GH, ND-G, US); San Juan Co., 2.5 km S. of Farmington, 20 May 1993, *Sivinski 2186* (BRY, UNM); UTAH: Kane Co., 43 km E. of Kanab, 6 Jun 1942, *Ripley and Barneby 4840* (GH); 6.5 km S. of Cannonville, 28 May 1965, *Cronquist 10212* (BRY, NY); San Juan Co., Monument Valley, Rock House, 17 May 1944, *Holmgren 3225* (GH).

1b. CRYPTANTHA FULVOCANESCENS (S. Watson) Payson var. NITIDA (Greene) Sivinski, stat. et comb. nov.—*Oreocarya nitida* Greene, Plantae Bakerianae 3:21. 1901.—TYPE: USA, Colorado, Mesa Co., Deer Run, 11 Jun 1901, *C. F. Baker 95* (lectotype, here designated: UC!; isolectotypes: GH!, POM!, RM!, US).

Indument white or fulvous with age. Cymes 5–11-flowered, obviously scorpioid, internodes evident. Fruiting pedicels 1–4 mm long. Calyx lobes slightly hispid and densely silky-strigose on abaxial surfaces, densely silvery strigose on adaxial surfaces. Nutlet surfaces usually covered with only rounded murications, occasionally with terminating setae. $n=12$.

Greene thought this taxon "noteworthy by the whiteness and softness of its almost satiny indument" though it can become fulvous with age or frost damage. The tallest and most satiny examples of this taxon occur in the canyon lands from Grand Junction, CO, to Moab, UT. As it ranges south, the plants lose some stature and length of indument. The *Baker 95* specimen at UC is designated as the lectotype because Greene referred only to the Deer Run, Colorado collection and was at UC at the time of publication.

Distribution. Western Colorado and eastern Utah, barely in northeastern Arizona and northwestern New Mexico (Fig. 1). On sandstone in piñon-juniper woodland and Great Basin Desert scrub at elevations from 1400 to 2300 meters.

Representative specimens. USA, ARIZONA: Navajo Co., near Kayenta along Hwy 164, 11 May 1972, *Higgins 5178* (BRY, WTSU).
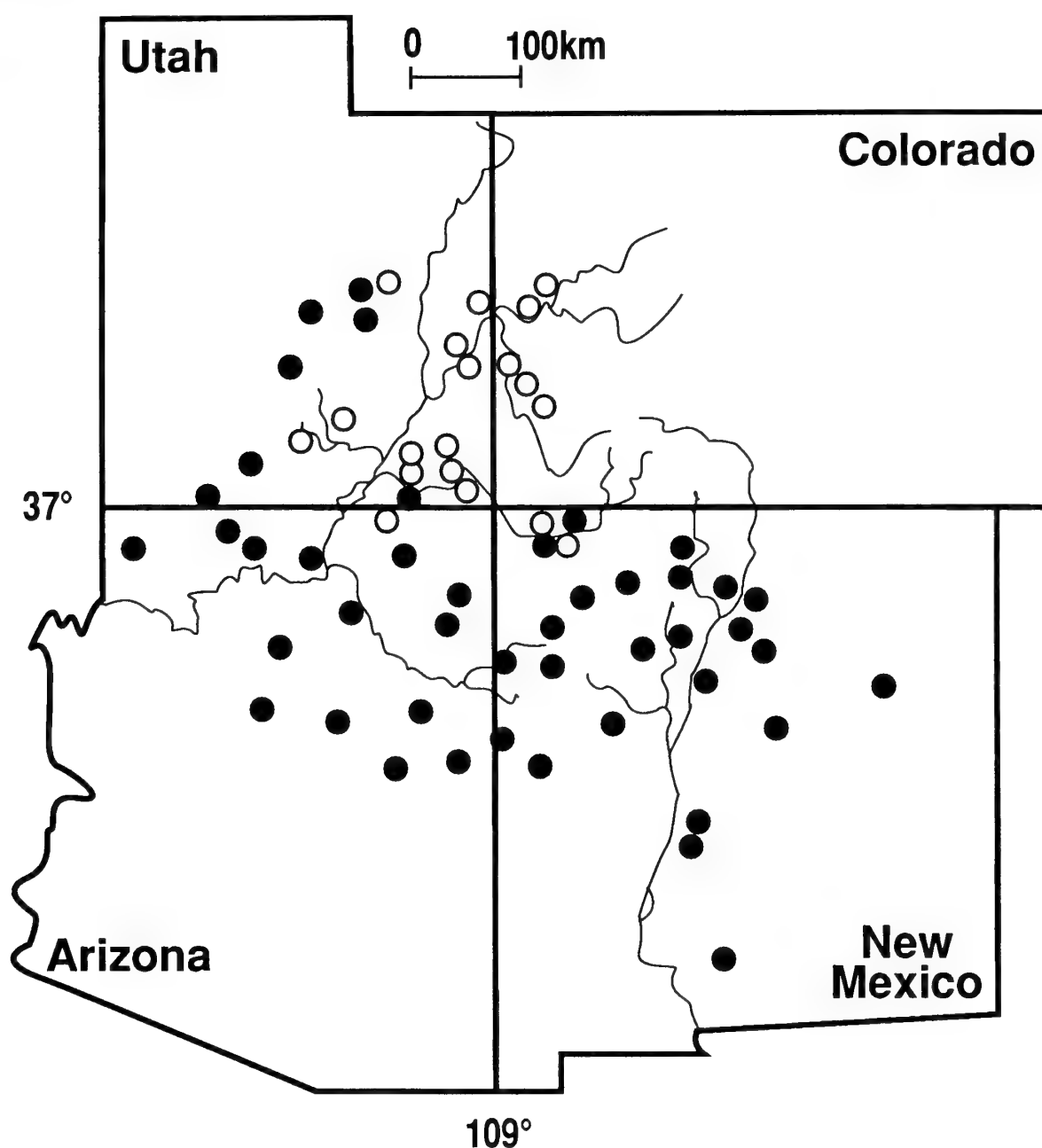
FIG. 1. Distribution of *C. fulvocanescens* var. *fulvocanescens* (solid circles) and *C. fulvocanescens* var. *nitida* (open circles) in the Four-corners region of Arizona, Colorado, New Mexico and Utah.

COLORADO: Mesa Co., Grand Junction, 17 May 1892, *Eastwood s.n.* (GH, RM, US); Mesa Co., hills south of Grand Junction, 11 Jun 1920, *Osterhout 6003* (GH, RM); Montrose Co., "gyp hills" at Paradox, 13 Jun 1912, *Walker 85* (GH, RM); Montrose Co., dry clay slopes on hills, 26 Jun 1924, *Payson and Payson 3876* (GH); San Miguel Co., Gypsum Valley, 6.4 km E. of Gypsum Gap, 9 Jun 1949, *Weber 4718* (COLO, GH, RM). NEW MEXICO: San Juan Co., Hwy 371, 2.5 km S of Farmington, 20 May 1993, *Sivinski 2185* (BRY, UNM). UTAH: Garfield Co., about 1.6 km E. of Waterpocket Fold, 72 km S. of Notom, 9 May 1965, *Cronquist 10053* (NY, RM); Grand Co., Cisco, 2 May 1890, *Jones s.n.* (RM, POM); San Juan Co., 15
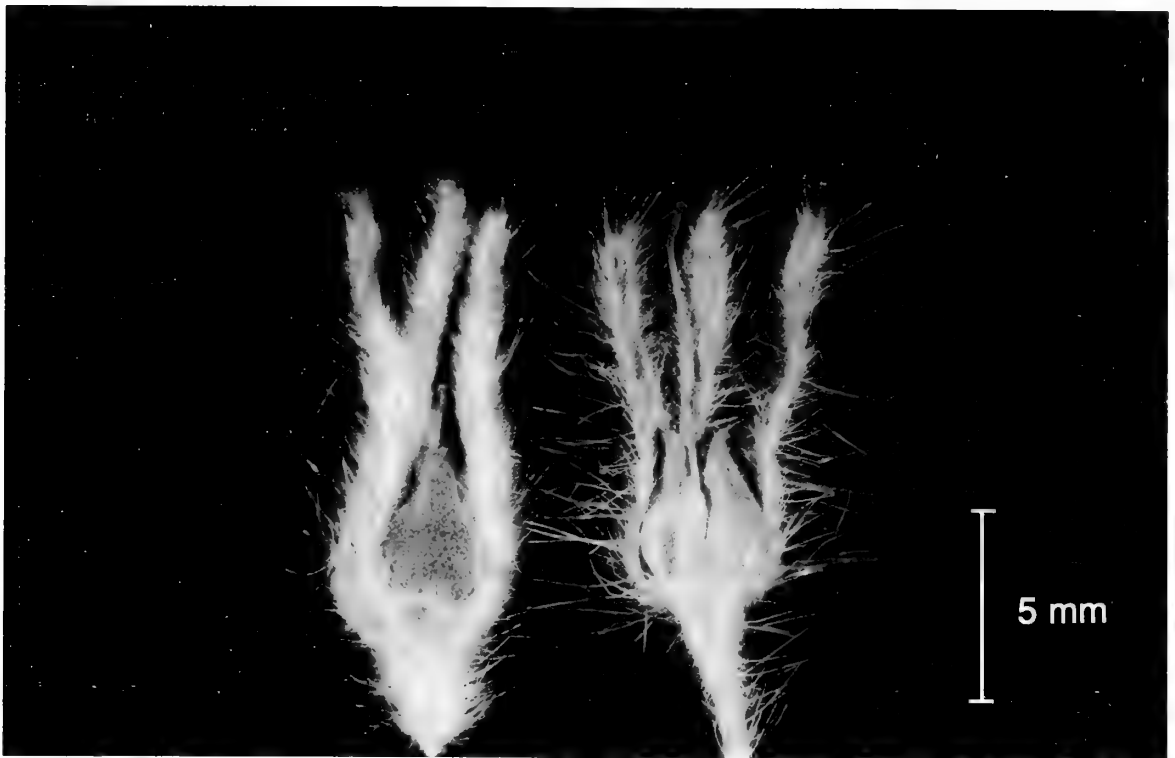
FIG. 2. Characteristic calyx pubescence for *Crypantha fulvocanescens* var. *nitida* (left) (*Sivinski 1211*, UNM) and *C. fulvocanescens* var. *fulvocanescens* (right) (*Clark 12748*, UNM).

km S. of Montezuma Creek on White Mesa Rd., 26 May 1983, *Hiel 1704* (BRY).

Cryptantha fulvocanescens vars. *fulvocanescens* and *nitida* are readily distinguishable in either flowering or fruiting stages. Variety *nitida* is usually larger in morphological features, although there is considerable overlap in measurements taken from the two varieties (Table 1). The notable exception is the range of pedicel length, which is usually shorter for var. *nitida* (0.8–4 mm) than var. *fulvocanescens* (2.5–8 mm). The combination of short pedicels, more flowers per cyme, and longer internodes between flowers gives var. *nitida* a longer, more narrow, scorpoid cyme than is typical of var. *fulvocanescens*. In flower or in fruit, var. *nitida* is distinguishable by the indument of its calyx lobes. The adaxial face of each lobe is so densely silvery-strigose that the green surfaces are completely obscured. In typical *fulvocanescens* the adaxial faces of the calyx lobes are only strigulose and the green surfaces are partly visible (Fig. 2). The density of setae on the nutlets of var. *fulvocanescens* is highly variable, but some murications with terminating setae are usually present, at least on the adaxial nutlet surface. In var. *nitida,* the nutlet murications are typically more rounded and without any terminating setae. Exceptional *nitida* populations with setose nutlets occur in southwestern Utah.

TABLE 1. MORPHOLOGICAL CHARACTERISTICS OF *CRYPTANTHA FULVOCANESCENS* VAR. *FULVOCANESCENS* AND VAR. *NITIDA*. Numbers of *fulvo-canescens* specimens examined from New Mexico = 28, Arizona = 20, Utah = 11. Specimens of *nitida* examined from Utah = 23, Colorado = 17, New Mexico = 3, Arizona = 1. Pedicel length measurements are from the oldest flower on the lowest cyme.

Character	var. *fulvocanescens*				var. *nitida*			
	n	Range	Mean	SD	n	Range	Mean	SD
Height (mm)	59	55–270	137	48	44	100–260	178	38
Flowers/cyme	59	2–7	4.3	1.2	44	4–11	6.3	1.7
Pedicel length (mm)	59	2.5–8.0	4.3	1.2	44	0.8–4.0	2.1	1.8
Fruiting calyx (mm)	47	5.2–12.0	8.8	1.3	29	8.2–13.2	10.2	1.5
Corolla tube (mm)	59	6.6–10.2	8.3	1.0	44	8.0–12.4	9.8	1.0
Nutlet length (mm)	47	3.1–4.0	3.4	0.3	29	3.4–4.4	3.8	0.3

Range and habitat preference are also different for these two taxa. Variety *nitida* grows almost exclusively on Colorado Plateau sandstones on the west slope of the Rocky Mountains and in the upper Colorado River Basin. Some var. *nitida* specimen labels indicate that the plants grow on shale. When those sites were revisited, however, the plants were found to be confined to gypseous, sandy soils or sandstones. Variety *fulvocanescens* has a much wider distributional range through Arizona, New Mexico, and Utah. It is not known from Western Colorado. It also occupies a wider variety of habitats, such as shales, clayey sands, and gypsum. The taxa are sympatric along the San Juan River of northwestern New Mexico and southeastern Utah. They grow together on the same outcropping slope approximately 2.5 km south of Farmington, NM. At that location, var. *nitida* grows only on sandstone strata and var. *fulvocanescens* occupies adjacent shale strata. Variety *fulvocanescens* at that location has a whiter indument than is normal for populations of the surrounding area.

Many of the historically early collections exhibit the extreme forms of a highly variable species and have contributed to the numerous efforts to maintain them as distinct species. The taxonomic distinctions become blurred in areas of sympatry in the Four-Corners region. In southeastern Utah and northeastern Arizona some var. *nitida* populations have longer pedicels and, occasionally, setose tips on the nutlet murications. Some northwestern New Mexico populations of var. *fulvocanescens* have unusually short pedicels and occasionally lack nutlet setae. When calyx pubescence is applied as the diagnostic criterion, however, a definite pattern emerges for geographic distribution and habitat substrate preference. Therefore, an understanding of the evolutionary progress of this species is better served by recognizing Greene's *nitida* at an infraspecific level rather than the more conservative approach of maintaining *C. fulvocanescens* as one highly polymorphic taxon.

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SYSTEMATICS OF THE *ACALYPHA CALIFORNICA* COMPLEX (EUPHORBIACEAE)

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ABSTRACT

The *Acalypha californica* complex (Euphorbiaceae) of the southwestern United States and northwestern Mexico has been treated as up to three species, *A. californica* Benth., *A. pringlei* S. Watson, and *A. stokesiae* Pax & K. Hoffm. Most recent authors, however, have recognized only two or one species, without offering supporting evidence. Study of herbarium specimens and population samples from throughout the range of the complex shows that most characters used to segregate the species cannot be used taxonomically because they vary either within individuals or within populations with no geographic pattern. In contrast, the frequency of plants with two distinct lengths of eglandular stem trichomes varies clinally. A different and weaker cline is followed by the number of teeth on the bracts subtending the carpellate flowers. Though in both clines the geographic extremes are different, no gaps in the clines are statistically recognizable. Only a single variable species, *A. californica,* should be recognized.

RESUMEN

El complejo *Acalypha californica* (Euphorbiaceae) del suroeste de los Estados Unidos y el noroeste de México ha sido tratado como tres especies, *A. californica* Benth., *A. pringlei* S. Watson, y *A. stokesiae* Pax & K. Hoffm. Sin embargo, autores recientes han reconosido solo una o dos especies, sin ofrecer evidencia apoyando este reconosimiento. El estudio de ejemplares del herbario y muestras de las populaciones de toda la distribución del complejo nos enseña que casi todas las características usadas para segregar las especies no deberian ser usadas taxonómicamente porque hay variación entre individuos o entre populaciones sin ningún diseño geográfico. Al contraste, la frecuencia de plantas con dos longitudes distintas de las tricomas del tallo eglandular varia gradualmente por toda su distribución. Una gradación diferente y débil se encuentra con el numero de dientes el las brácteas que subténden las flores femeninas. Aunque en las dos gradaciones los extremos geográficos son diferentes, ningunas de las aberturas son reconocidas estadísticamente. Solo una especie variable, *A. californica,* deberia ser reconocida.

Most floras (e.g., Wheeler 1942, 1960; Wiggins 1964; Munz 1974; Webster 1993) recognize two shrubby species of *Acalypha* L. (Euphorbiaceae) in the southwestern United States: *A. californica* Benth. in California and *A. pringlei* S. Watson in Arizona. Some authors (Miller 1964; Felger et al. 1992), however, have treated these as a single species, though without presenting supporting evidence. A

third species in this alliance, *A. stokesiae* Pax & K. Hoffm., has also been described, but most authors have overlooked this name. While preparing a treatment of the *Acalypha* of Arizona (Levin in press), I undertook field and herbarium studies to test whether these species, which I will call the *A. californica* complex, are distinct. I present those results here.

Acalypha californica was described in 1844 from a specimen collected in Baja California Sur, Mexico (Bentham 1844), and by 1891 was known to range from San Diego County, California, to the Cape Region of Baja California (Watson 1880; Brandegee 1891). Meanwhile, Watson (1885) described *A. pringlei* from a specimen from northwestern Sonora, Mexico. Despite his familiarity with *A. californica,* Watson compared his new species not with this species, but with two from central Mexico. Later, Pax and Hoffmann (1924) reported *A. californica* from Sonora and described *A. stokesiae* (as *stokesii*) from southern California, comparing it (in their key only) with species from South America. The reported range of *A. pringlei* was extended to Arizona by Tidestrom and Kittell (1941) and Wheeler (1942).

Only three publications have dealt with two or more of these names, and each treatment is different. Pax and Hoffmann (1924) recognized three species in the *A. californica* complex and used differences in inflorescence structure to place them in three separate "series," groups taxonomists today probably would equate with sections (cf. Webster 1967). According to their monograph, *A. californica* has strictly axillary inflorescences that are carpellate, staminate, or sometimes androgynous (carpellate below and staminate above); *A. pringlei* has terminal and axillary carpellate inflorescences and axillary staminate (rarely androgynous) inflorescences; and *A. stokesiae* has strictly axillary inflorescences that are either carpellate or androgynous. The androgynous inflorescences of all three species were reported to produce few carpellate flowers. Wiggins (1964) recognized two species, placing *A. stokesiae* in synonymy under *A. californica.* He distinguished *A. californica* from *A. pringlei* based on *A. californica* having (1) the stems with eglandular trichomes of uniform length vs. with some eglandular trichomes at least twice as long as those forming most of the pubescence; (2) the leaf bases cordate vs. truncate or rounded, or rarely cordate; (3) the young foliage often viscid vs. not viscid; and (4) the bracts subtending the carpellate flowers with 15–21 teeth vs. 9–11 teeth. Miller (1964), studying specimens principally from the United States, stated that she could find no differences between *A. californica* and *A. pringlei* but that field work was needed in Mexico; she did not mention *A. stokesiae.* Felger et al. (1992) implicitly recognized only a single species when they reported the shrubby *Acalypha* from southern Arizona as *A. californica,* but they listed no synonyms.

MATERIALS AND METHODS

Herbarium specimens of *Acalypha californica* and *A. pringlei* were borrowed from A, ARIZ, ASU, B, BM, CAS, DAV, DES, DS, F, GH, MICH, MIN, MO, NY, POM, RSA, SD, UC, UCR, and US; I could locate no specimens labeled *A. stokesiae* even with special requests to herbaria known to have Susan Stokes' collections (Lanjouw and Stafleu 1986). On the 356 specimens that had both new growth and fairly precise locality data, I measured trichome lengths using a Wild M–8 dissecting microscope with an ocular micrometer. I examined new growth near the stem tips to ensure that trichomes had not been lost as the stem weathered or as bark was produced. On the 249 specimens that also had mature bracts subtending carpellate flowers, I counted the number of teeth on three to five bracts oriented so that all teeth were visible. I also studied inflorescence sexuality and position and leaf shape on all herbarium specimens.

To study variation within populations I collected samples from 18 populations in California, Arizona, Baja California, and Sonora; collection data appear in the Appendix. In each population I collected one stem with new growth from each of 20 shrubs scattered through the population. These specimens are deposited at SD. I measured trichomes and counted bract teeth using the same protocol as for the herbarium specimens. Though it seemed impractical to quantify viscidness, while in the field I handled the young foliage in an attempt to subjectively assess how sticky it was.

I preserved some young stems in FAA (formalin-acetic acid-ethanol) from one population each in California, Baja California, and Sonora. To study trichome morphology I cut free-hand cross sections of the preserved stems with a razor blade, mounted the unstained sections on a microscope slide, and examined them with a Nikon Labophot compound microscope.

Statistical analyses. I analyzed geographic variation in the frequency of indument types using the χ^2 test for independence using actual proportions (Zar 1984). Where I found significant differences, I then did multiple comparisons using a Tukey-type test for proportions (Zar 1984). For this test I normalized the proportions using the modified arcsine transformation Zar (1984, formula 14.5) recommended be used when many proportions are large or small, as was the case with these data. I tested for geographic differences in numbers of bract teeth using the Kruskal-Wallis single factor analysis of variance by ranks, followed by non-parametric multiple comparisons using the Tukey test with the ranked data (Zar 1984). Because my sample sizes were large, I used Student's t-test with unequal variances to determine if numbers of bract teeth differed between plants with different indument types. These analyses were carried out using spreadsheet and statistical functions in Quattro Pro for

Windows (Borland International, Inc. 1993). To further test the strength of the geographic patterns observed, I performed a discriminant analysis with cross validation using Systat for Windows (Systat, Inc. 1992).

RESULTS

Inflorescence position and sexuality. Throughout the range of the *A. californica* complex, many plants produce both terminal and axillary inflorescences. Terminal inflorescences are uniformly carpellate, but apparently are not produced consistently by every plant. Axillary inflorescences predominate and may be staminate, carpellate, or androgynous with 1–3 carpellate flowers at the base; all three types frequently are present on a single plant. Occasional plants bear a single carpellate flower at the apex of staminate or androgynous inflorescences.

Leaf base shape. The shape of the leaf bases in the *A. californica* complex is quite variable. Even on the same plant they may be cordate, rounded, truncate, or occasionally obtuse. Because the variability within plants made this character of little taxonomic value, I did not try to quantify base shape.

Foliage viscidness. I was unable to find any consistent differences in foliage viscidness throughout the geographic range of the *A. californica* complex. This characteristic may be primarily environmentally determined: leaves produced on lush growth under good growing conditions often were viscid whereas those produced under drier or hotter conditions were not.

Stem trichome morphology. All plants in the *A. californica* complex produce two types of trichomes on their stems, glandular and eglandular. Glandular trichomes are multiseriate with a stalk about four cells across and several cells long bearing a spherical to oblate multicellular head. These trichomes are yellowish in color and 0.05–0.2 mm (rarely to 0.5 mm) long. Eglandular trichomes are uniseriate. Lengths are quite variable, ranging from 0.1 to 1.2 mm, with the shortest trichomes consisting of as few as two cells and longest of as many as seven cells. Other than cell number, I saw no morphological differences between short and long trichomes.

The lengths of the eglandular stem trichomes on individual plants fell into three basic patterns. In the first pattern, found on 208 (58%) of the 356 herbarium specimens examined, the trichome lengths showed little variation, with the range no more than 0.2 mm; on all but six of these specimens the trichomes were all less than 0.3 mm long. Of the specimens with more variation, most (117, 33% of total specimens) showed the second pattern, bearing short (0.1–0.3 mm long) trichomes mixed with others 2–10 times as long. Only 31 (9%)
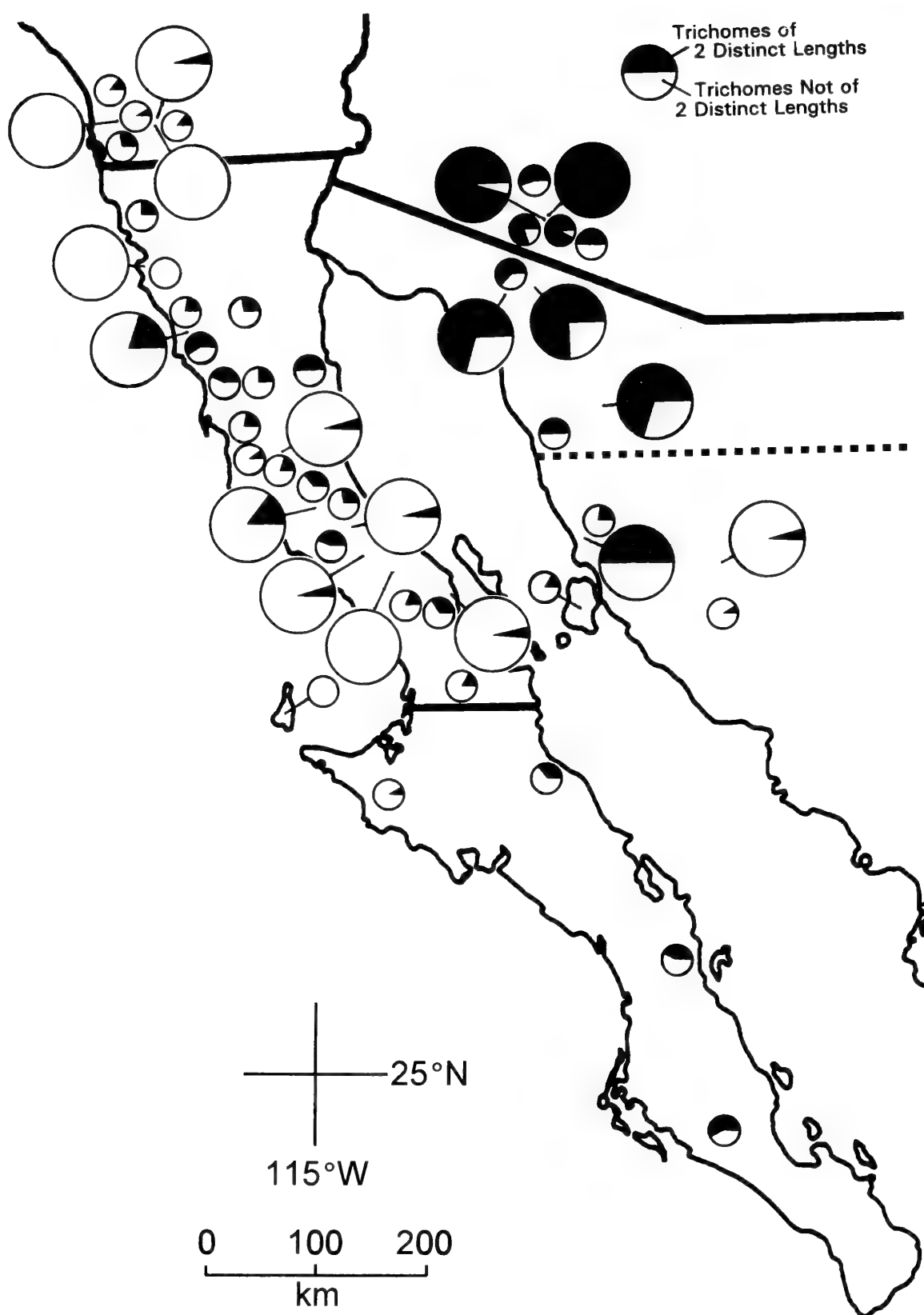
Fig. 1. Southwestern United States and northwestern Mexico showing geographic variation within the *Acalypha californica* complex in the frequency of plants with two distinct lengths of eglandular stem trichomes. Small pie charts are based on herbarium specimens; 7–14 herbarium specimens from the same geographic region were grouped and a pie chart placed at their mean position. Large pie charts summarize population samples of 20 plants each. The dashed line in Sonora represents 30°N latitude.

TABLE 1. REGIONAL VARIATION IN STEM INDUMENT AND BRACT TOOTHING SHOWN BY HERBARIUM SPECIMENS OF THE *ACALYPHA CALIFORNICA* COMPLEX. Sample sizes are shown in parentheses; not all specimens had mature bracts so these sample sizes are smaller. Values followed by the same superscript letter are not statistically different (multiple comparisons using Tukey test with arcsine transformed proportions (stem indument) or ranked data (bract toothing), P > 0.05).

Region	Frequency of specimens with two distinct lengths of eglandular stem trichomes	Mean number of bract teeth
California	16.7% (36)[a]	13.24 (19)[ab]
Sonora south of 30°N	16.7% (30)[a]	12.69 (21)[ab]
Baja California	26.4% (178)[ab]	13.69 (127)[a]
Baja California Sur	36.7% (49)[bc]	13.61 (36)[ab]
Sonora north of 30°N	54.5% (22)[cd]	12.68 (14)[b]
Arizona	70.7% (41)[d]	12.62 (32)[b]

specimens had the third pattern, trichomes that varied continuously in length with a range >0.2 mm. The population samples showed the same three patterns, again with very few individuals showing continuous variation. Because the frequencies of continuous variation in trichome length were small and close to statistical expectations, this class had little impact on the statistical analyses that follow; the same test results were obtained recognizing this class or combining it with either of the other two classes. For ease of data presentation and interpretation, I therefore recognized two categories of specimens: those with two distinct lengths of eglandular stem trichomes and those with little or continuous variation in length. This division parallels Wiggins' (1964) distinction between *A. pringlei* and *A. californica*.

In no case did different branches of a single plant show different patterns of eglandular stem trichome lengths. However herbarium specimens from nearby locations often differed, with the frequency of the two classes varying geographically (Fig. 1). To test whether this variation was statistically significant, I divided the specimens into six geographic areas (Table 1): Arizona, Baja California (Norte), Baja California Sur, California, northern Sonora (north of 30°N latitude), and central Sonora (south of 30°). I separated Sonora into these two areas because of Wiggins' (1964) statement that only *A. pringlei* grows in the northern part of the state whereas both *A. californica* and *A. pringlei* grow in the central region. The frequencies were not independent of geography (χ^2 = 42.88, df = 5, P < 0.001), but formed a cline with the frequency of specimens with two distinct lengths of eglandular stem trichomes being lowest in California and increasing through Baja California, Baja California Sur, northern

TABLE 2. FREQUENCY OF PLANTS WITH TWO DISTINCT LENGTHS OF EGLANDULAR STEM TRICHOMES IN POPULATIONS OF THE *ACALYPHA CALIFORNICA* COMPLEX. Each population is represented by 20 plants. Populations are numbered with my collection numbers; detailed locality information appears in the Appendix. Populations followed by the same superscript letter are not statistically different (multiple comparisons using Tukey test with arcsine transformed proportions, P > 0.05).

Locality	Frequency (%)
California: 2152[a]	0
California: 2192[a]	0
Baja California: 2130[a]	0
Baja California: 2141[a]	0
California: 2150[ab]	5
Baja California: 2134[ab]	5
Baja California: 2138[ab]	5
Baja California: 2140[ab]	5
Baja California: 2145[ab]	5
Sonora (south of 30°): 2190[ab]	5
Baja California: 2137[ab]	15
Baja California: 2133[bc]	20
Sonora (south of 30°): 2187[cd]	50
Sonora (north of 30°); 2173[d]	70
Sonora (north of 30°): 2191[d]	70
Sonora (north of 30°): 2156[de]	75
Arizona: 2154[ef]	95
Arizona: 2155[f]	100

Sonora, to Arizona. Adjacent areas in this cline did not differ, whereas more distant areas were significantly different (Table 1). Central Sonora had a lower frequency of specimens with two distinct lengths of eglandular stem trichomes than did northern Sonora, but the frequency did not differ from that found in Baja California and California (Table 1).

Individual plants from the same population also often had different patterns of eglandular stem trichome lengths (Fig. 1, Table 2), and the frequency of plants with two distinct lengths of eglandular stem trichomes was not independent of population ($\chi^2 = 217$, df = 17, P < 0.001). When the populations were sorted by frequency, they showed a cline generally similar to that shown by the specimens (Table 2). In both Baja California and central Sonora, however, there were significant differences among populations from the same region, indicating that there is considerable local variation within the overall cline, a pattern also shown by the herbarium specimens (Fig. 1) and reflected in the results of the discriminant analysis (see below). In addition, there was less association of populations from central Sonora with those from Baja California and California than there was with the herbarium specimens, perhaps as a consequence of more restricted sampling with the populations (two samples from inland

areas) than with the specimens (30 specimens from a wide geographic area).

Bract tooth number. The number of teeth on the bracts subtending the carpellate flowers varied from eight to 21, with lower numbers generally in Arizona and Sonora and higher numbers generally in Baja California and California (Table 1). Herbarium specimens from the six geographic regions differed significantly (Kruskal-Wallis test: $H = 16.919$, df $= 5$, P < 0.01). The sequence of geographic regions was different from that shown by the eglandular stem trichome lengths, however, and only the extremes (Arizona and northern Sonora vs. Baja California) differed statistically (Table 1). The number of bract teeth did not differ between specimens in the two trichome classes (Student's t $= 0.795$, df $= 141$, P [two-tailed] $= 0.43$), further showing the weak association between bract toothing and stem trichome characteristics. Too few plants in the population samples bore mature bracts to use these for statistical tests.

Discriminant analysis. Another way to evaluate these geographic patterns is through discriminant analysis with cross validation. In this procedure, a portion of the data is used to construct a discriminant function. For cross validation, this function is then used to predict the group assignments of the remaining portion of the original data. The more accurately the predicted assignments reflect actual group membership, the better the data distinguish among the groups. Using the herbarium specimens and data on both trichome type and bract toothing, I tested two scales of geographic classification. In each case I randomly selected approximately half the specimens for the analysis and used the remaining specimens for cross validation. When the specimens were sorted into the six geographic regions discussed above, 52% of the specimens were assigned to their correct regions during cross validation. However, when the specimens were sorted into the 35 groups represented by the small pie charts in Figure 1, only 8% of the specimens were correctly assigned. Therefore eglandular trichome pattern and bract toothing separate large regions moderately well, but local regions poorly. Stated differently, there may be statistically significant clines in these characters, but the clines are weak and subject to considerable local variation.

DISCUSSION

When Pax and Hoffmann (1924) revised *Acalypha,* they examined very little Mexican material (McVaugh 1961), indeed only three specimens in the *A. californica* complex (two of *A. californica,* one of *A. stokesiae,* and none of *A. pringlei*). Study of more material invalidates the supposed differences in inflorescence position and

sexuality that Pax and Hoffmann used to place these species in three different subgeneric groups. This error is symptomatic of the overall weakness of their classification, in which they emphasized mechanical separation of species by key characters, often at the expense of showing taxonomic relationships (Standley and Steyermark 1949).

Among the characteristics that Wiggins (1964) used to distinguish *A. californica* and *A. pringlei,* both leaf shape and herbage viscidness vary widely within and among individual plants. More significant are the differences in eglandular stem trichome lengths and bract tooth number, both of which show clinal variation. Plants from California form one extreme ("*A. californica*") and those from Arizona form the other ("*A. pringlei*"), but plants from intermediate locations bridge the gap. From an ecological standpoint, these differences may reflect adaptation to different selective pressures, as has been shown with some other clines (e.g., Jones 1973; Briggs and Schultz 1990). Trichomes may be important in defense against herbivores (Ågren and Schemske 1993) or in drought tolerance (Ehleringer 1984). They may instead be genetically linked with other characteristics that are adaptive (Ågren and Schemske 1994), which might be the case also with bract tooth number, which has no obvious adaptive function. I have no direct evidence that either of these traits is genetically rather than environmentally controlled, but specimens (*Balls 19566, 18869; Campbell 20504; Gibson 1636; Shultz 4900*) taken from plants grown at the Rancho Santa Ana Botanical Garden in Claremont, CA, do not vary in either trait from each other or from their maternal parent collected in San Diego County, California (*Wolf 9490*).

From a taxonomic standpoint, two conclusions could be drawn from my analysis of these data. First, this complex could consist of two broadly sympatric species that differ morphologically almost exclusively in trichome features, with one species being more common at one end of the distribution and the other species at the other end. Both species would exhibit the same pattern of geographic variation in bract tooth number. Alternatively, there could be a single species with clinal variation in eglandular stem trichome lengths and bract tooth number. I find the second conclusion more plausible, because I think it unlikely both (1) that two sympatric species of wind-pollinated perennial plants would differ in such a trivial characteristic as trichome type and (2) that bract tooth number would show the same geographic pattern in two distinct species. In the absence of evidence to the contrary, I conclude that this complex consists of a single species. The prevalence of variation both within populations and among nearby populations (Fig. 1) argues against recognition even of infraspecific taxa. Instead, I agree with Miller (1964) that the *A. californica* complex should be treated as a single variable species, with the following synonymy:

Acalypha californica Benth., Bot. Voy. Sulph. 51. 1844. *Ricinocarpus californicus* (Benth.) Kuntze, Revis Gen. Pl. 2:617. 1891.—TYPE: MEXICO, Lower California [Baja California Sur], Magdalena Bay, hills, October–November 1839, *G. W. Barclay* (lectotype, BM! [photos DS!, NY!, POM!]; isolectotypes K, LE, MIN!, MO!, RSA!, U; lectotype designated here).

Acalypha pringlei S. Wats., Proc. Amer. Acad. Arts 20:373. 1885.— TYPE: MEXICO, Sonora, ravines, shore of Gulf of California, 29 March 1884, *C. G. Pringle* (holotype, GH!; isotypes, A!, CAS!, F[2]!, MICH!, NY[2]!, US[3]!).

Acalypha stokesiae [as "*stokesii*"] Pax & K. Hoffm., Pflanzenreich IV. 147. xvi. (Heft 85) 138. 1924.—TYPE: USA, California, San Diego Co., San Diego, *S. Stokes* (holotype, B†; no photographs or isotypes found). I have seen no specimens with this name, but there is no other *Acalypha* in San Diego Co. Designating a neotype seems unnecessary.

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Appendix

Collection data for *Acalypha californica* population samples.

Levin 2130: MEXICO, Baja California, Punta Banda, 7 km S of Hwy. 23 along dirt road branching from road to Los Arbolitos, 31°41′N, 116°31′W, 300 m, 14 October 1991.

Levin 2133: MEXICO, Baja California, Hwy. 1, 20.8 km SE of San Vicente, 31°10′N, 116°08′W, 200 m, 14 October 1991.

Levin 2134: MEXICO, Baja California, Hwy. 1, 20.2 km E of El Rosario, 30°03′N, 115°33′W, 300 m, 15 October 1991.

Levin 2137: MEXICO, Baja California, Hwy. 1 just S of Sonora, where wash crosses road, 29°54′N, 114°56′W, 650 m, 15 October 1991.

Levin 2138: MEXICO, Baja California, Hwy. 1, ca. 6 km NW of Hotel La Pinta, Cataviña, 29°47′N, 114°48′W, 600 m, 16 October 1991.

Levin 2140: MEXICO, Baja California, 17.9 km SE of Hotel La Pinta, Cataviña, 29°39′N, 114°37′W, 715 m, 16 October 1991.

Levin 2141: MEXICO, Baja California, Hwy. 1, 13 km SE of Nueva Chapala and 35.7 km NW of turnoff to Bahía de Los Angeles, 29°19′N, 114°21′W, 625 m, 16 October 1991.

Levin 2145: MEXICO, Baja California, 6.6 km NW of Bahía de Los Angeles at Arroyo Columpia, 28°59′N, 113°36′W, 180 m, 17 October 1991.

Levin 2150: USA, California, San Diego Co., Anza-Borrego Desert State Park, unnamed canyon draining N side of Inner Pasture, crossing Hwy. S-2 just N of June Wash, 32°56′N, 116°16′W, 365–395 m, 8 April 1992.

Levin 2152: USA, California, San Diego Co., Anza-Borrego Desert State Park, Indian Gorge 1.5 km W of Hwy. S-2, 32°52′N, 116°13′W, 275 m, 8 April 1992.

Levin 2154: USA, Arizona, Pima Co., Organ Pipe Cactus National Monument, Ajo Mountain Drive about 5 km NE of Hwy. 85, near junction of loop, 31°58′N, 112°47′W, 540 m, 12 April 1992.

Levin 2155: USA, Arizona, Pima Co., Organ Pipe Cactus National Monument, Estes Canyon, 32°01′N, 112°42′W, 730–755 m, 12 April 1992.

Levin 2156: MEXICO, Sonora, Mun. Puerto Peñasco, Hwy. 2, 17.7 km S of Sonoyta near where ridge of Sierra Cubabi approaches road, 31°43′N, 112°51′W, 500 m, 13 April 1992.

Levin 2173: MEXICO, Sonora, Mun. Pitiquito, 16 km S of Pitiquito on road to Puerto de la Libertad, 30°32′N, 112°01′W, 350 m, 14 April 1992.

Levin 2187: MEXICO, Sonora, Mun. Pitiquito, 101 km NW of Morelos on hwy. to Puerto de la Libertad, ca. 4.5 km SE of turnoff to San Ignacio, 29°36′N, 112°16′W, 200 m, 16 April 1992.

Levin 2190: MEXICO, Sonora, Mun. Hermosillo, N of Hermosillo at junction of Hwy. 15 and Hwy. 21, 29°10′N, 110°55′W, 300 m, 17 April 1992.

Levin 2191: MEXICO, Sonora, Mun. Puerto Peñasco, Hwy. 8 18.4 km SW of Sonoyta (Hwy. 2), near SW end of Sierra Cipriano, 31°46′N, 113°00′W, 400 m, 17 April 1992.

Levin 2192: USA, California, San Diego Co., Poway, W slope of Twin Peaks, E of E end of Monte Vista Rd., 32°59′N, 117°03′W, 200–230 m, 27 May 1992.

SOME OBSERVATIONS ON POLLINATION IN MEXICAN ASCLEPIADACEAE

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Abstract

Flower-insect interaction was studied in three Mexican asclepiad species, a member of the *Matelea reticulata* complex, *Cynanchum foetidum* and *Funastrum arenarium*. In the *Matelea reticulata* population, flies were the only visitors observed; and they were carrying pollinaria. Several young fruits were found in the population. Only honeybees were seen in the population of *Cynanchum foetidum*. These naturalized bees did not achieve pollinia transfer, but instead destroyed the flowers they visited. *Funastrum arenarium* was visited during the day by honeybees, which caused no destruction in this large-flowered species. A heavy perfume, intensifying towards the evening, indicated an adaptation for night-moth pollination. Small night-moths were observed carrying pollinaria. A comparatively high pollinia insertion rate and ample fruit set were observed.

Resumen

En el presente artículo se describen las interacciónes entre flores e insectos en tres especies mexicanas de la familia Asclepiadaceae: un representante del complejo *Matelea reticulata, Cynanchum foetidum* y *Funastrum arenarium*. En la población de *M. reticulata,* los únicos visitantes observados fueron moscas. Las mismas transportaron polinarios y la población produjo frutos. La población de *C. foetidum* fue visitada exclusivamente por abejas. Estas abejas naturalizadas no transfirieron polinios y destruyeron las flores que visitaron. *Funastrum arenarium* tambien fue visitada por abejas durante el día, pero no destruyeron las flores grandes de esta especie. Al llegar la noche, el perfume muy dulce de estas flores aumentó, indicando una adaptación para la polinizicición de mariposas nocturnas. Se observo una proporción de inserción de polinios comparablamente alta, y las planta produjeron amplias frutas.

The complex pollination mechanism in the Asclepiadaceae has long received attention (Brown 1833). Thus, the general mechanism of pollination is fairly well understood and is only briefly outlined here. In all higher asclepiads, the pollen grains are united into a pollinium. In the Asclepiadoideae, each of the five anthers contains two pollinia, and the pollinia of two adjacent anthers are united into a pollinarium by means of two caudicles and a central corpusculum (cf. Kunze 1993). The central corpusculum is arranged atop two adjacent, stiffened margins of the anthers (anther wings). If a body part of a nectar seeking insect is caught between the anther wings, the insect can only free itself by performing an upward motion with

its caught body part; a downward motion is in most cases prevented by structural devices of the flower (e.g., upwardly directed bristles). Thus, the trapped body part is directed into the corpuscular cleft which clamps onto the insect. The motion of the insect removes the corpusculum, to which the pollinia are attached. Pollinia from pollinaria which are already attached to the insect body from previous flower visits may be inserted between the anther wings during the same operation. After insertion of one pollinium, the whole pollinarium either becomes detached from the insect, or the inserted pollinium breaks off and the second pollinium of the pollinarium is free to be inserted between a different pair of anther wings. Of course, this description only outlines the general process of asclepiad pollination, and there are numerous possibilities preventing pollinia transfer in a specific case. If, e.g., insect size and flower size are not correlated, the insect might either get stuck in the guide rail lacking the force needed to free itself, or it might slip through without removing the pollinarium. Also, the pollinia might break off the corpusculum during pollinarium removal, or during other activities of the insect. Finally, pollinia might not be deposited in a position allowing the pollen tubes to reach the stigmatic surfaces.

More than 50 publications are available studying details of pollination in the genus *Asclepias,* and only a small sample can be listed here (e.g., Broyles and Wyatt 1991; Kephart 1981; Willson et al. 1979). In contrast, observations in other taxa are by far less numerous. Meve and Liede (1994) provide a review of pollination in the myiophilous[1] Old World tribe Stapelieae. The large-flowered genus *Calotropis* (tribe Asclepiadeae) and its pollinator *Xylocopa* have been studied in some detail (e.g., Wanntorp 1974), and a few observations on Australian (e.g., Forster 1992) and Indian Marsdeniaeae and Asclepiadeae (e.g., Chaturvedi and Pant 1986) are strewn through the literature. For Latin America, the study of Skutch (1988) on the Gonolobeae *Fischeria* DC. and some observations on *Sarcostemma* (*Funastrum*; Kunze and Liede 1991) are the only published records known to me. One reason for this lack of attention might lie in the scattered occurrence and the low individual density of populations especially in the twining members of the family. Recent expeditions to Mexico allowed some observations, which, though rather preliminary and by no means complete, shed some light on the diversity of flower-insect interaction in the family.

[1] The term myiophily is derived from the Greek μψια, meaning fly or mosquito. Delpino (1868) italianized the term to miophil. Vogel (1954), apparently without checking the original source, transcribed it into the German miophyil. The mistake has been perpetuated by subsequent authors.

Fig. 1. A. *Matelea reticulata* in habitat; B. *Matelea reticulata* flower, with flies visiting.

MATERIALS AND METHODS

Flowering populations of *M. reticulata* and *C. foetidum* were observed during the day (9.30 a.m.–14.30 p.m.) near Santa Cruz Etla, Oaxaca, Mexico in excellent weather conditions (27/28 July 1989). *Funastrum arenarium* was observed between 8.30 a.m. and 20.00 p.m. near San Carlos, Baja California Sur, Mexico (14 Jan 1992), also in excellent weather conditions.

Visitors were caught, placed into a clear plastic bag, stunned with a whiff of alcohol vapor, and checked for pollinia with a handlens (10× magnification). To limit the amount of damage done to the local insect fauna, insects not carrying pollinaria were set free. Pollinaria-carrying insects were sent for identification to Dr. P. de Vries, University of Texas, and Dr. W. La Berge, Natural History Survey, University of Illinois.

At the end of each observation, inflorescences containing open and wilted flowers were preserved in 70% EtOH. Removed pollinaria and inserted pollinia were counted under a dissecting microscope. Plant vouchers were deposited at MO.

OBSERVATIONS

Matelea reticulata. The *Matelea reticulata* (Engelm. ex A. Gray) Woods. complex is widespread in Texas and northern to central Mexico. The form studied (Fig. 1A, B), however, is restricted to a few valleys in Central Mexico, where it is rather abundant (Stevens personal communication). *Matelea* Aublet belongs to the tribe Gonolobeae K. Schum., the only tribe of the Asclepiadaceae restricted to the New World.

Matelea reticulata possesses relatively large flowers (ca. 1.5 cm diam.) on long pedicels in few-flowered, umbelliform inflorescences. The maximum number of open flowers at any given time does not exceed six. The cream corolla lobes, patterned with a dense network of green and brown lines, are basally fused, and spread almost horizontally. The shining yellow gynostegium contrasts sharply against this dull background (Fig. 1B). Neither scent nor nectar could be detected.

The population studied must have been in flower for quite some time as judged by several young fruits and numerous wilted flowers. Though insect activity was considerable during observation, an average of only 0.94 pollinaria per flower were removed (Table 1). Compared with other Asclepiadaceae (2.5 pollinaria per flower in Mexican *Funastrum* [*Sarcostemma* subg. *Ceramanthus*], Kunze and Liede 1991; 3.6 pollinaria/flower in Northern American *Asclepias* spp., Lynch 1977; Willson and Rathke 1974) this is a low removal rate. In contrast to reports from several species of *Asclepias* (e.g., Chaplin and Walker 1982; Willson and Rathke 1974), pollinaria removal did not increase with umbel size (Table 1b). In contrast, the number of removed pollinaria showed a tendency to decrease with umbel size, but not significantly (r = −0.80, t = −1.87, P > 0.1). The percentage of flowers with no removed pollinaria did not change significantly with umbel size (r = 0.11, t = 0.16, P > 0.4). Double removals accounted for as many removed pollinaria as single removals (35.5% each), while triple and quadruple removals together accounted for the rest. There was a tendency for double removals becoming more frequent with increasing umbel size (r = −0.82, t = −2.05, P > 0.05). Insertion rate was also comparatively low at 0.19 pollinia per flower; thus, on the average, only one of five flowers received a pollinium. Twenty pollinia were inserted in stigmatic chambers above which the residual pollinarium was still in place, and ten in stigmatic chambers above which the residual pollinarium was missing. Double insertions were scarce (2 of 161 flowers) and multiple insertions did not occur. However, the presence of young fruits in the population indicates that this low insertion rate is still sufficient for fruit-set and thus, propagation.

Only flies were observed visiting the flowers of *M. reticulata* (Fig. 1B). The flies, all approximately of the size of a house fly, belong to the Calliphoridae (*Phaenicia sericata* [Meigen]), Muscidae and Tachinidae. Pollinia were found exclusively on the labella of the haustellum. Recently, I have observed Calliphoridae visiting a South American member of the tribe Gonolobeae, *Gonolobus argentinensis* T. Mey.

Cynanchum foetidum. *Cynanchum foetidum* H.B.K. (Fig. 2), subtribe Cynanchinae, tribe Asclepiadeae, is widespread over southern

TABLE 1A. POLLINARIA REMOVAL AND POLLINIA INSERTION IN *M. RETICULATA* (LIEDE & CONRAD 2588).

Removed pollinaria per flower	No. of flowers	% of flowers 161 = 100%	Removed pollinaria	% removed pollinaria 805 = 100%	Inserted pollinia	% inserted pollinia 805 = 100%
0	67	41.61	0	0	8	0.99
1	54	33.54	54	6.70	9	1.11
2	27	16.77	54	6.70	8	0.99
3	8	4.97	24	2.98	4	0.49
4	5	3.11	20	2.48	1	0.12
5	0	0.00	0	0.00	0	0.00
Total	161	100.00	152	18.86	30	3.00

TABLE 1B. POLLINARIA REMOVAL AND INFLORESCENCE SIZE IN *M. RETICULATA* (LIEDE & CONRAD 2588).

Removed pollinaria per flower	Open flowers/inflorescence				No. of flowers
	1	2	3	>3	
No. infl. (n = 72)	11	39	17	5	
Total flowers	11	78	51	21	161
0	4	34	21	8	67
1	3	25	17	9	54
2	1	13	10	3	27
3	2	4	2	1	8
4	2	2	1	0	5
5	0	0	0	0	0
Total poll. (n = 152)	16	71	47	18	
Poll./infl.	1.5	1.8	2.8	3.6	
Poll./flower	1.5	0.91	0.92	0.85	

and central Mexico. Like *M. reticulata,* it prefers medium altitudes (to 1500 m) and slightly ruderal habitats where it grows in densely tangled masses over other shrubbery, walls and fences (Fig. 2A).

Cynanchum foetidum H.B.K. possesses small flowers (ca. 0.7 cm diam.; Fig. 2B) borne in a bostrychoid cymose inflorescence. The maximum number of flowers open at the same time was six. In open flowers the creamy white adaxial surfaces of the strongly recurved corolla lobes face the observer, thus contrasting with the yellowish abaxial surfaces displayed by buds. Access to the gynostegium is inhibited by the rather large, five-tipped corona. The flowers emit a very sweet, honey-like odor and contain a copious amount of nectar.

Judged from numerous wilted flowers, the population studied must have been in flower for quite some time. However, no young fruits

FIG. 2.   A. *Cynanchum foetidum* H.B.K. in habitat; B. *Apis mellifera* on flower of *Cynanchum foetidum*.

were found. Pollinaria removal rate (Table 1) was almost equal to the one of *M. reticulata* (0.87 pollinaria per flower). Double removals were accounting for as many removals as single and triple removals together. In this species, flowers broke off easily, so that the umbel size could be determined only for 60% of all flowers counted. In these 60%, again, a non-significant tendency for pollinaria removal decreasing with inflorescence size was found (Table 2b; $r = -0.76$, $t = -2.00$, $P > 0.05$). There was also a non-significant tendency for the number of flowers with no removed pollinaria to increase with umbel size ($r = 0.78$, $t = 2.15$, $P > 0.05$). Pollinia insertion rate was extremely low—two pollinia in 117 flowers (0.02 pollinia per flower).

During the time of observation, *C. foetidum* was visited intensively and exclusively by the honeybee, *Apis mellifera* L., which is not native to the Americas. Of the ten bees examined, eight carried between one and three pollinaria which were attached to the distal parts of the proboscis by the corpusculum.

During morphological examination of the flowers, hardly any intact open flower could be found. Commonly, the stylar head was detached from the remainder of the gynostegium, and the slender tips of the two ovaries were broken. It is known that this damage was not done during process of counting the removed and inserted pollinia, because uncounted flowers displayed the same damage.

Funastrum arenarium. Funastrum arenarium (Decne. ex Benth.) Liede ined. is a very attractive species endemic to Baja California, where it inhabits open spots of old sand dunes (Fig. 3A). At the point of this writing, this taxon poses a nomenclatural problem. Holm (1950) in his revision of the genus, placed this species, along

TABLE 2A. POLLINARIA REMOVAL AND POLLINIA INSERTION IN *C. FOETIDUM* (LIEDE & CONRAD 2587).

Removed pollinaria per flower	No. of flowers	% of flowers 117 = 100%	Removed pollinaria	% removed pollinaria 585 × 100%	Inserted pollinia	% inserted pollinia 585 = 100%
0	57	48.72	0	0.00	0	0.00
1	26	22.23	26	6.05	2	0.34
2	26	22.23	52	8.89	0	0.00
3	8	6.83	24	4.00	0	0.00
4	0	0.00	0	0.00	0	0.00
5	0	0.00	0	0.00	0	0.00
Total	117	100.00	102	18.94	2	0.34

TABLE 2B. POLLINARIA REMOVAL AND INFLORESCENCE SIZE IN *C. FOETIDUM* (LIEDE & CONRAD 2587).

Removed pollinaria per flower	Open flowers/inflorescence						No. of flowers
	1	2	3	4	>4	?	
No. infl. (n = 22)	3	4	9	3	3	—	
Total flowers	3	8	27	12	16	51	117
0	0	4	12	6	9	26	57
1	1	1	7	4	3	10	26
2	1	3	7	1	2	12	26
3	1	0	1	1	2	3	8
4	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0
Total poll. (n = 102)	6	7	24	9	13	43	
Poll./infl.	2.0	1.75	2.6	3.0	4.3	—	
Poll./flower	2.0	0.87	0.88	0.75	0.81	0.84	

with the species of *Funastrum* Fourn. in *Sarcostemma* subg. *Ceramanthus* Kunze sensu Holm. Evidence from latex triterpenoid analysis (Liede and Mahlberg unpublished) and from DNA analysis (Liede et al. unpublished), however, show that Holm's (1950) concept of *Sacrostemma* is untenable and that *Funastrum* should be resurrected. Until this is formally done, the taxon will be referred to as *Funastrum arenarium* (Decne. ex Benth.) Liede ined.

Funastrum arenarium possesses showy, large (ca. 1.5 cm diam.) flowers in dense, semiglobose, umbelliform inflorescences of 9–16 flowers. All flowers open at the same time (Fig. 3B). The patent to horizontal, finely ciliate corolla lobes are dark red, with a pronounced white margin. The white staminal corona is topped by a protruding dark red stylar head. The nectariferous flowers exhale a heavy, sweetish perfume with a strong carnation component, and intensifies as the evening approaches.
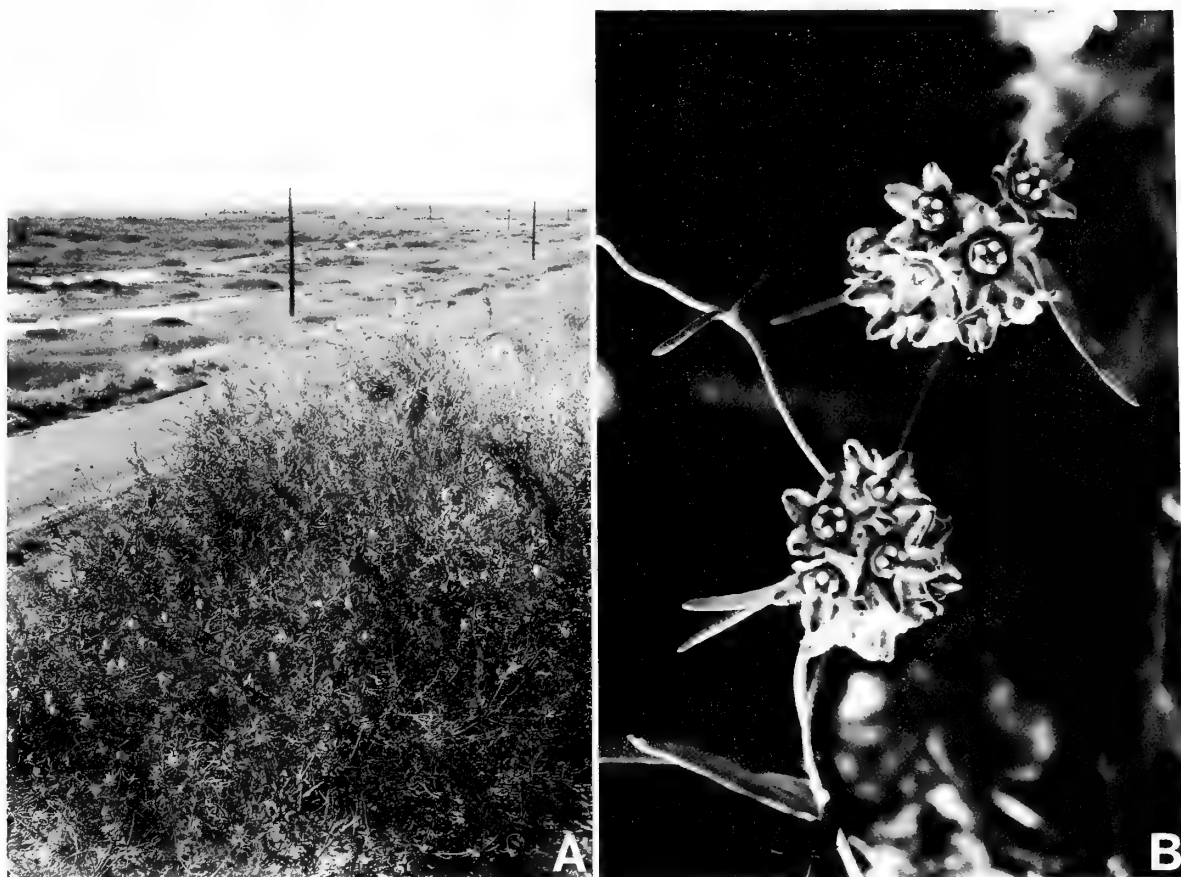
FIG. 3.   A. *Funastrum arenarium* in habitat; B. *Funastrum arenarium* flowers.

In the population studied numerous fruits in all stages of maturity were found, indicating that the population had been flowering for at least several weeks. Both pollinaria removal and pollinia insertion rate were found to be very high—2.68 pollinaria and 2.01 pollinia per flower, respectively. Of the 101 flowers counted, only 15 had neither a pollinarium removed nor a pollinium inserted, but four flowers had all five pollinaria removed, as well five pollinia inserted. Three removals and two or three insertions were the most frequent condition. Inserted pollinia were found more frequently in stigmatic chambers above which the residual pollinarium was still in place; incomplete removal of pollinaria was observed in several cases. As flowers were very easily detached from the inflorescence, the number of umbels remaining for analysis was low (n = 8). As far as any conclusions are possible from this low number, with increasing number of flowers per inflorescence, there is a tendency for a decrease in removal rate (r = 0.89, t = 2.77, P > 0.05) and a tendency for an increase of flowers without removed pollinaria (r = 0.89, t = 2.77, P > 0.05). Similar results were obtained in *F. pannosum* (Decne.) Schltr. and *F. clausum* (Jacq.) Schltr. (*Sacrostemma* subg. *Ceramanthus,* Kunze and Liede 1991).

During daytime, honeybees were visiting the flowers almost incessantly. The ten bees caught were carrying between two and seven

TABLE 3A. POLLINARIA REMOVAL AND POLLINIA INSERTION IN *F. ARENARIUM* (LIEDE & CONRAD 2952).

Removed pollinaria	No. of flowers	% of flowers 101 = 100%	Removed pollinaria	% removed pollinaria 505 = 100%	Inserted pollinia	% inserted pollinia 505 = 100%
0	20	19.80	0	0.00	6	1.18
1	6	5.94	6	1.19	6	1.18
2	9	8.91	18	3.56	20	3.96
3	31	30.69	93	18.42	70	13.86
4	21	20.80	84	16.63	55	10.89
5	14	13.86	70	13.86	46	9.10
Total	101	100.00	271	53.66	203	40.17

TABLE 3B. POLLINARIA REMOVAL AND INFLORESCENCE SIZE IN *F. ARENARIUM* (LIEDE & CONRAD 2952).

Removed pollinaria	Open flowers/inflorescence					No. of flowers
	3	4	5	>5	?	
No. infl. (n = 8)	2	1	4	1	—	
Total flowers	6	4	20	8	63	101
0	0	1	4	6	9	20
1	2	0	1	1	2	6
2	0	0	2	0	7	9
3	2	1	6	1	21	31
4	2	1	4	0	14	21
5	0	1	3	0	10	14
Total poll. (n = 271)	16	12	54	4	185	
Poll./infl.	8.0	12.0	13.5	2.0	—	
Poll./flower	2.66	3.00	2.70	0.5	2.93	

pollinaria on the distal parts of their legs; a preference for any particular pair of extremities could not be discovered. No pollinaria were found on the mouth parts. At dusk, several small night-moths (wing span 2–3 cm) were observed on the flowers, and the one caught was carrying a pollinarium on the distal part of the front leg.

CONCLUSIONS

The observations reported here suggest that there is, in fact, a remarkable diversity of pollinator spectra and pollination syndromes in Mexican Asclepiadaceae. For *M. reticulata* the present observations support the indications of myiophily derived from floral characteristics (myiophilous syndrome, Vogel 1954). While myiophily is quite frequent in the family—all of the African Stapeliads are known to be myiophilous and the myiophilous syndrome (Vogel

1954) can be observed in several African members of the tribe Asclepiadeae—this is the first case to be reported from the Americas. However, the myiophilous syndrome can be observed in other members of the tribe Gonolobeae, but needs confirmation from field observations.

In *C. foetidum,* a potential case of destructive nectar-robbery has been detected. *Apis mellifera* is not simply exploiting the nectar of *C. foetidum* without accomplishing pollinia exchange, as has been recorded for a number of visitors on *Asclepias verticillata* L. (Willson et al. 1979), but seems to destroy the flowers it visits. While almost all bees were found to carry pollinaria, there were only two inserted pollinaria in 117 flowers and no young fruits could be found. This indicates that, while the bees can remove pollinaria, they fall short of inserting pollinia. In larger flowers, the illegitimate visitors often pay for the intrusion with their lives (Robertson 1887); however, the flowers of *C. foetidum* are certainly too small to effectively trap as strong an insect as a honeybee. The damage observed in the flowers indicates that the bees, if they get entangled, free themselves by force, destroying the flower in the process. Thus, the legitimate pollinator(s) have no chance to accomplish successful pollination. Also, the legitimate pollinator(s) are probably of much smaller body size and will not patronize a population in which numerous honeybees are busy foraging (compare Westerkamp 1991). The impact of honeybees on *C. foetidum* and its natural pollinators needs a systematic follow-up over a larger area to assess the impact of this badly adapted visitor on the species as a whole.

The pollination syndrome of *F. arenarium* differs slightly from the one observed in *F. clausum* and *F. pannosum* (Kunze and Liede 1991). While the floral perfume of the *F. clausum* and *F. pannosum* is very sweet without being heavy, the perfume of *F. arenarium* has a distinct heavy carnation-like component, thus indicating a shift to moth pollination, which was confirmed during this observation. During the day, *F. clausum* and *F. pannosum* were visited by hesperid butterflies, bees, Diptera, and moths. A similar allotropous visitor spectrum of bees, skippers and butterflies has been reported for *Fischeria,* a large-flowered (exceeding 2.5 cm diam.) member of the tribe Gonolobeae (Skutch 1988). In contrast, only honeybees were observed on *F. arenarium.*

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POLLINATION BIOLOGY OF THE RARE SHRUB *FREMONTODENDRON DECUMBENS* (STERCULIACEAE)

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ABSTRACT

Pollination is crucial to successful sexual reproduction in plants. I studied the pollination biology of the rare shrub *Fremontodendron decumbens* to obtain basic information on floral traits and behavior, determine the importance of floral visitors to seed production, assess pollen limitation of reproductive success, and identify and characterize the behavior of floral visitors. Flowers opened for about 3 days, and photographs of floral UV reflectance revealed a ring-like pattern that was interpreted as aiding in the efficiency of pollinator visits. Many flowers (25%) were pollinated prior to anther dehiscence, and essentially 100% were pollinated by the time anther dehiscence was completed. Insect visitation was required for pollination. Hand pollination did not increase fruit set but almost doubled seed number per fruit. Even hand-pollinated flowers contained many undeveloped ovules, indicating that pollen limitation was not the only factor limiting seed production. The anthophorid bee *Tetralonia stretchii* was the primary floral visitor. This species, together with the megachilid bee *Callanthidium illustre,* accounted for 98% of 1746 observed floral visits. The abundance and behavior of these bees indicated they were the major pollinators of *F. decumbens* flowers. Given the importance of these bees as pollinators, I concluded that preservation of this rare species must include preservation of its pollinating fauna of native solitary bees.

Much effort in conservation biology is expended to ensure adequate levels of reproduction in rare species. In plants, successful sexual reproduction requires survival of flowers and seeds through several potentially hazardous life-history stages, including flower bud production, pollination, fruit maturation, seed dispersal, and germination/establishment (Boyd and Brum 1983a, b).

Insect-mediated pollination may be of critical importance to sexual reproduction in rare plants. In a review of the reproductive traits of rare plants of Utah, Colorado, and California, Harper (1979) concluded that most rare plant taxa rely upon insect pollination. He suggested that survival of many rare plants depends on maintenance of adequate pollinator populations. However, pollination studies of rare plants are, with some exceptions (e.g., Johnson 1992; Kevan et al. 1991; Lesica 1993), themselves rather scarce. This may leave a critical gap in the knowledge needed to effectively manage both rare plant populations and their animal mutualists.

Fremontodendron decumbens R. M. Lloyd is a rare shrub endemic to gabbro-derived soils that support an unusual type of chaparral vegetation in California (Hunter and Horenstein 1992). The species was described fairly recently (Lloyd 1965) and was confirmed as distinct from the other two species in the genus by a recent revision of *Fremontodendron* (Kelman 1991). A recent study by Boyd and Serafini (1992) showed that seed production in *F. decumbens* was severely limited by insect predation. They found that most (>97%) of the flower buds, flowers, and fruits produced by *F. decumbens* were destroyed by insects. However, survival of flowers to the fruit stage was relatively high, implying that successful pollination was achieved relatively frequently.

This study was designed to complement the work of Boyd and Serafini (1992) by investigating the flower/fruit transition in *F. decumbens*. Besides scattered studies (e.g., Fulton and Carpenter 1979; Young 1972), little specific information is available on the pollination biology of many chaparral species, including species of *Fremontodendron* (Scogin 1979). We know of no published work on the pollination biology of *F. decumbens,* despite the potential value of this knowledge to conservation and management of this rare plant. This study was undertaken to span this gap in knowledge of the biology of *F. decumbens.* Specific objectives were to: 1) describe floral features important to pollination biology, including UV reflectance patterns and floral behavior, 2) determine the importance of floral visitation to fruit set, 3) investigate the role of pollen limitation in determining reproductive output of *F. decumbens,* 4) identify important insect pollinators of *F. decumbens,* and, 5) describe the importance of pollination biology to conservation strategies for *F. decumbens.*

METHODS

The study site was Pine Hill in the foothills of the western Sierra Nevada, El Dorado County, California. This location is the type locality for *F. decumbens* (Lloyd 1965). Most individuals of the species are located on rocky ridgetops within 1 km of the summit of Pine Hill (Boyd and Serafini 1992) and are included in a small (16.2 ha) ecological reserve managed by the California Department of Fish and Game. *Fremontodendron decumbens* occupies chaparral areas dominated by *Adenostoma fasciculatum* and *Arctostaphylos viscida.* Even in its most abundant stands, it is a minor constituent (<5% cover) of the chaparral in these areas. This species is a small (<2 m tall) shrub that produces abundant, relatively large (3–5 cm diameter), copper/orange to yellow flowers during late spring and early summer (Kelman 1991). Flowers are apetalous but have five petaloid sepals, each with a nectary at its base (Kelman 1991). Ad-

ditional descriptions of the study area and study species have been presented by Lloyd (1965), Kelman (1991), and Boyd and Serafini (1992). Excepting some of the floral visitor surveys, studies reported in this paper were performed at Site 1 of Boyd and Serafini (1992) because this site includes the largest number of *F. decumbens* on Pine Hill.

Preliminary observations of floral behavior showed that anthesis could be divided into five stages based on positions of the sepals and dehiscence of the anthers. The stage of anthesis at which flowers were naturally pollinated was examined by enclosing flowers in different stages of anthesis and determining the frequency of fruit production for flowers enclosed during each stage. During mid-June 1983, 17 branch sections containing one or more flowers representative of these five stages were selected in the late afternoon. This time of day was chosen so that flowers were available to insect visitors during the morning and afternoon of the day of the experiment. Flower peduncles were marked with colored wire. Besides ten unmanipulated flowers in the first stage of anthesis that were present on the branches, an additional seven first stage flowers were marked with two lengths of wire and hand-pollinated with anthers from a flower of another shrub. The hand-pollinated flowers were included to determine whether pollination at the earliest stage of anthesis would result in fruit formation. Branches then were covered with cheesecloth enclosures. Enclosures were removed after 3 weeks, and the number of those flowers in each stage of anthesis that had become fruits was recorded. Following Boyd and Serafini (1992), the beginning of the fruit stage was defined by the separation of the anther cap (fused stamen filaments covering the ovary) from the rest of the flower.

Floral patterns in ultraviolet (UV) wavelengths were examined by taking UV-light photographs using standard black and white film. A 35-mm single-lens reflex camera was fitted with a Corning CF-760 filter. This filter transmits longwave UV (300–400 nm) with peak UV transmittance in the 350–370 nm range. The same flower was also photographed without using the UV filter. A gray scale was included in each photograph to ensure correct exposure and minimize the risk of misinterpreting visualized patterns (Kevan 1979).

The importance of floral visitors to pollination was tested by excluding visitors from flowers using cheesecloth enclosures. In mid-June 1982, 17 branches were selected, each one bearing at least one flower bud near anthesis and at least one open flower or fruit. Open flowers and immature fruits were marked with a different color of wire than unopened buds. Branches then were covered with cheesecloth enclosures for two months. When enclosures were removed, wire color was used to distinguish between fruits produced by flowers that opened inside the enclosure and flowers that had opened prior

TABLE 1. DESCRIPTIONS OF STAGES OF ANTHESIS OF *F. DECUMBENS* FLOWERS AND PERCENTAGE OF FLOWERS IN EACH STAGE POLLINATED DURING OR PRIOR TO THAT STAGE.

Stage #	Flower stage description	Percent fruiting (n)
1	Open, but sepals reflexed <45 degrees	10 (10)
2	Sepals reflexed >45 degrees but no anther dehiscence	25 (8)
3	At least one anther dehisced but prior to dehiscence of all anthers	100 (9)
4	All anthers dehisced, sepals still fully reflexed	94 (16)
5	Flower senescing, sepals wilting (reflexed <45 degrees)	91 (11)

to enclosure construction. Frequency of fruit production by the two groups of flowers was compared by contingency table analysis.

Pollination limitation of fruit set was examined in mid-June 1983. Twenty pairs of flowers in early stages of anthesis were marked with lengths of colored wire. One flower of each pair was selected randomly to be hand pollinated three times a day for two days. Hand pollination was performed by applying pollen directly to stigmas using freshly-dehisced anthers taken from flowers of nearby shrubs. Three weeks later all flowers were examined for evidence of fruit formation.

Pollen limitation of seed production was examined in mid-June 1982. Forty-four flowers beginning anthesis were marked and hand-pollinated three times daily for two days. The fruits produced were collected one month later and the number of seeds in each was counted. To compare seed production by hand-pollinated flowers with seed production by naturally-pollinated flowers, a collection of 178 fruits was made from many (>25) shrubs in late July and the number of seeds in each was counted.

Ovule counts of flowers were made for comparison to the numbers of seeds matured by fruits. In mid-June 1982, a newly-opened flower was collected arbitrarily from each of 45 shrubs. Ovaries were dissected and the number of ovules in each was recorded.

Preliminary observations indicated that only a few bee species visited flowers consistently. The relative importance of these species was determined by monitoring floral visits in June of 1982 and 1983. Two methods were used: either a cluster of shrubs containing many open flowers was observed or the area of the study site with the greatest shrub density (Site 1 of Boyd and Serafini 1992) was actively patrolled. Surveys were made by one or two observers. Surveys lasted 30 minutes each and were performed at different times during the period when bee activity was greatest (1000–1700 hr). Observations

of the behavior of bees visiting flowers were recorded. Five censuses were performed in 1982, and four in 1983. All censuses took place on Pine Hill, except for one in 1983 performed on a small population of *F. decumbens* located <1 km west of the summit of Pine Hill. Representative specimens of the bees observed were captured for later identification.

Results

Flowers progressed through the five stages of anthesis (Table 1) in three days or less. In some cases, the style elongated so that the stigma projected beyond the sepals when the opening at the apex of the calyx was only a few millimeters wide. The sepals continued to reflex until they formed a slight cup or became nearly flat. Shortly after the flower had completely opened, anther dehiscence began and continued for about a day. By the end of the second or third day, the sepals wilted and closed back loosely over the stamens and style.

At least one enclosed flower from each stage of anthesis developed into a fruit. Flowers at the earliest stage of anthesis (stage 1, Table 1) were pollinated infrequently. Only one of ten flowers developed a fruit despite flowers at this stage being capable of successful pollination. Five of the seven (71%) hand-pollinated stage 1 flowers included in enclosures developed fruits. The failure of most naturally-pollinated stage 1 flowers in enclosures to produce fruits must be attributed to their not having been pollinated prior to placement of the enclosure. Fully 25% of the flowers that had completely opened but had not yet dehisced any anthers (stage 2) were pollinated and, therefore, must have received pollen from another flower. This result also implies that the pollinator of these flowers must have received only a nectar reward because pollen in a stage 2 flower was not available for harvesting (Table 1). Essentially all flowers had been pollinated by the time all anthers had dehisced (stage 3 and beyond, Table 1).

Ultraviolet light photographs revealed a striking floral pattern that accentuated the pattern observable in visible light (Fig. 1). Distal portions of the sepals, which were yellow-orange to orange-red in visible light, were UV reflective. In contrast, a small portion of the proximal area of the sepals, all parts of the stamens, and all of the style were UV absorbent. Stamens, style and the nectary at the base of each sepal were yellow-colored in visible light. The area of UV absorbance at the base of the sepals included the nectary. Stamens, pollen, style, and foliage were also UV absorbent. Thus, individual flowers viewed from above in UV light appeared as a wide, bright ring around a dark center. The dark center contained the nectaries and the sexual parts of the flower.

None of 39 enclosed flower buds produced fruits when they opened

within enclosures, indicating that floral visitors were required for pollination. The microenvironment in the enclosures (shading, etc.) did not prevent fruit development because 32% of the 22 flowers that had opened prior to enclosure construction produced fruits. The difference in frequency of fruit production between flowers opening inside the enclosures and pre-existing flowers or fruits was statistically significant (contingency table analysis, P = 0.0046).

Hand-pollination did not significantly improve fruit set. Seventy percent of 20 open-pollinated flowers and 80% of 20 hand-pollinated flowers set fruits. These frequencies were not significantly different (contingency table analysis, P = 0.973). However, hand-pollination did significantly increase seed production per fruit (Mann-Whitney U test, P = 0.0001). Mean seed production per fruit was 1.9 times higher in the 30 hand-pollinated fruits than in the 178 open-pollinated fruits (respectively, 4.9 ± 3.5 versus 2.6 ± 3.4 seeds per fruit, means ± SD).

Examination of placentas of mature fruits usually showed some undeveloped ovules. Flowers contained many more ovules (21.6 ± 4.33, mean ± SD) than became mature seeds, even in fruits produced following hand-pollination of flowers. Fruits from hand-pollinated flowers that lacked insect damage (in undamaged fruits complete placentas could be viewed) only averaged 6.3 ± 4.1 seeds (mean ± SD). This difference between the number of ovules counted in flowers and the seed production of undamaged fruits produced from hand-pollinated flowers was highly significant (Mann-Whitney U test, P = 0.0001).

Almost all (99%) of the 1746 observed floral visits were made by native solitary bees. The majority of the visits (89.4%) were by the anthophorid bee *Tetralonia stretchii* (Cresson). Males and females of this genus are easily differentiated because males have very long antennae (Timberlake 1969). Of the 1560 visits by this species, 90% were made by females. Second in importance (8.7% of the total visits) was the megachilid bee *Callanthidium illustre* (Cresson).

In general, both of these bee species behaved similarly during floral visits. A typical visit began with a bee arriving at the center of a flower by landing on top of the stamens. A pollen-collecting bee would gather pollen from the anthers with its legs while remaining on the upper portion of the flower. Nectar-collecting bees, particularly male *Tetralonia,* would also land on top of the stamens. They would then lean downward toward the nectaries, holding onto the stamens, and probe a nectary. Lateral movement around the stamens allowed them to probe each of the nectaries in turn. Movements of both female and male bees appeared to bring their venters into contact with both anthers and stigma as they worked flowers for nectar and/or pollen rewards.

Fig. 1.   *Fremontodendron decumbens* flower in stage 4 of anthesis, showing visible light (above) and ultraviolet light (below) reflective patterns. The gray scale is included to demonstrate correct exposure of each photograph.

Less than 2% of the visits were made by a variety of other bees. Honeybees (*Apis mellifera* L.) accounted for 1% of the visits. Some small halictid bees also were observed on the flowers. They were relatively infrequent visitors during the surveys, accounting for 0.44% of the visits. Captured specimens were identified as *Lasioglossum sisymbrii* (Cockrell), *Dialictus punctatoventris* (Crawford), and a species of *Evylaeus*. A few visits (0.46%) from *Bombus californicus* Smith also were recorded. Visits by the halictid bees and *Bombus*

were observed only during the 1983 surveys. Based on both size and behavior, the halictid bees were probably not effective pollinators of *F. decumbens* flowers. The few individuals observed collected pollen from individual anthers. These bees were so small that they were able to crawl onto individual anthers without contacting the stigma. On the other hand, *Bombus* individuals were large enough to have been effective pollinators.

A few other infrequent visitors were observed at times other than the visitor survey periods. Hummingbirds were observed hovering near flowers several times during the two flowering seasons, and contact with flowers was observed once. These visits seemed incidental, however, as the birds did not remain near flowers very long before flying away. Syrphid flies were also observed licking pollen from anthers a few times outside of the census periods.

DISCUSSION

Scogin (1979) reported that the quantity and sugar concentration of nectar from flowers of *Fremontodendron californicum* (Torrey) Cov. and *F. mexicanum* Davidson, the other two species in the genus, fit the general features of bird-pollinated plants. Although we occasionally observed hummingbirds at our study site, insect floral visitors predominated. Although visits to flowers do not necessarily lead to pollination (e.g., Motten et al. 1981), the evidence available in this case is compelling. The visitation frequency and behavior of the two most frequent insect visitors, *Tetralonia stretchii* and *Callanthidium illustre,* strongly suggest that they are the primary pollinators of *F. decumbens.*

To my knowledge this is the only study of the floral visitors of *F. decumbens.* There is some information on visitors to flowers of other *Fremontodendron* species. Timberlake (1969) reported three male *T. stretchii* from *Fremontodendron* flowers in Madera County, California. These individuals must have been visiting flowers of *F. californicum,* the only *Fremontodendron* species reported from that county (Kelman 1991). In a broad review of pollination ecology in California, Moldenke (1976) lists carpenter bees in the genus *Xylocopa* as visiting flowers of *Fremontodendron* (species unspecified), along with an unspecified assortment of generalist feeding bees. In general, it appears that flowers of *Fremontodendron* are primarily visited by bees and that bees pollinate flowers of this genus.

The reliance of *Fremontodendron* on bees for pollination is not surprising. Mediterranean-climate shrublands have diverse pollinator faunas in general (Herrera 1988; Moldenke 1976) and support diverse bee faunas in particular (Moldenke 1976). Moldenke (1976) suggests that competition by pollinators for floral resources is intense due to the high diversity and abundance of pollinators in chaparral

areas. The large unspecialized flowers of *Fremontodendron* represent a significant resource readily available to foraging bees.

Fremontodendron decumbens flowers have several traits that make them rich food sources readily located and used by bees. Boyd and Serafini (1992) estimated that a typical shrub on this study site opened 300 flowers during a single reproductive season. Flowers of *F. decumbens* are large relative to those produced by many chaparral shrubs (i.e., *Adenostoma, Arctostaphylos, Ceanothus*), with correspondingly large nectaries and anthers. Hence the amount of pollen and nectar available from a visit to a single flower is probably relatively high. Support for this conclusion is provided by Scogin (1979), who reported that nectar from a single flower of *F. californicum* may provide 11–16.5 mg sugar. This is a relatively large quantity for a single flower of a bee-pollinated plant (Heinrich 1975).

The results of this study explain the relatively large proportion (75%) of *F. decumbens* flowers that become fruits, as reported by Boyd and Serafini (1992). Because of the attractive features of *F. decumbens* flowers, bees were efficient in pollinating individual flowers. Many flowers (25%) were pollinated prior to anther dehiscence. Furthermore, hand-pollination did not increase significantly the frequency of fruit set relative to open-pollinated flowers, indicating that bees pollinated essentially every open flower.

Ultraviolet light reflectance patterns are widely recognized as adaptations that enable visiting insects to more efficiently locate and manipulate flowers (Silberglied 1979). The UV reflectance of the sepals of *F. decumbens,* in combination with the UV absorbance displayed by the centers of flowers, makes a circular pattern that may indicate to bees where nectar and pollen resources are located. The behavior of *C. illustre* and *T. stretchii,* which usually landed on a flower at its center, suggests that the UV pattern aided in orienting visiting bees. On a larger scale, contrast of the UV reflectance of sepals against the UV absorbance of foliage of *F. decumbens* may assist bees in discriminating flowers from foliage. Thorp et al. (1975) also reported UV nectar fluorescence in flowers of *Fremontodendron californicum* and *F. mexicanum.* They suggested that nectar fluorescence was a visual cue whereby bees could evaluate availability of nectar before landing on a flower and thereby increase foraging efficiency.

Despite the apparent efficiency of bees in visiting and pollinating the great majority of flowers, seed production of individual flowers was pollen-limited. Pollen limitation has been documented for many species (Lee 1988), including other rare plants (e.g., Timmerman-Erskine 1992). Management actions that result in increased pollinator abundance may increase plant reproductive output in a pollen-limited species. However, the large number of undeveloped ovules in fruits of *F. decumbens* produced from hand-pollinated flowers

indicates additional constraints on reproductive output. One pos-
sibility is that resource availability is inadequate for additional seeds
to develop. Herrera (1988) suggested that resource limitation is a
community-level feature in Mediterranean-climate shrublands. This
resource limitation may have adaptive significance in forcing de-
veloping seeds to compete for resources so that only seeds with
greater fitness survive (Lee 1988). A second possible function of the
large ovule-to-seed ratio is to provide an opportunity for maternal
selection of fertilized ovules (Doust and Doust 1988). The impor-
tance of either of these phenomena to sexual reproduction of *F.
decumbens* is unknown.

Conservation of rare plant species may be problematic because
individuals in a protected area may require wide-ranging animals
to perform important ecologic functions, such as pollination or seed
dispersal (Cox et al. 1991). For example, a recent study by Lesica
(1993) documented the importance of bee pollination to the fitness
of an endangered plant, concluding that effective management of the
plant must include management of pollinator populations. For *F.
decumbens,* the conservation implication of the study reported here
is clear. *Fremontodendron decumbens* is pollinated by native solitary
bees and requires bees for pollination. Management of areas con-
taining *F. decumbens* therefore must include management of the bee
fauna of those areas.

Management of the bee fauna requires specific information on
habitat requirements of the bees, but little specific information on
habitat requirements of *Callanthidium* and *Tetralonia* is available.
Both bee species are polylectic and have been collected from a variety
of spring-flowering species (Krombein et al. 1979). In a monograph
on the genus, Timberlake (1969) reported *T. stretchii* to be "rather
rare." He reported specimens from flowers of several genera of plants,
including three individuals collected in Madera County from flowers
of *F. californicum.* Floral visitation records for *C. illustre* are more
numerous and include a wide variety of plant species (Krombein et
al. 1979).

Information on the nesting biology of these solitary bees is even
more limited. In general, members of the Megachilidae either ex-
cavate nest cavities in wood or build nests in a wide variety of pre-
existing cavities (O'Toole and Raw 1991). The Anthophoridae typ-
ically nest in chambers excavated in the ground (O'Toole and Raw
1991). Hicks (1929) described nesting of *C. illustre* in dead stems
and stumps and suggested that bees might forage at some distance
from nesting sites. I can find no specific information on the nesting
biology of *T. stretchii,* which may be a reflection of the rarity of this
species (Timberlake 1969).

In summary, there is little information on the habitat requirements
of these bees. It seems likely that they forage on a variety of plants

(including *F. decumbens*) that may occur at some distance from their nesting locations. Therefore, management of these bee species may need to include consideration of land-use practices on privately-owned areas adjacent to the Pine Hill Ecological Reserve.

Even under optimal management regimes, events that cannot be controlled by the managing agency (e.g., fire, off-site development, etc.) might decrease abundance of these native bees. However, even complete destruction of the bees that pollinate *F. decumbens* will not necessarily limit pollination. Pollination mutualisms either may or may not be species-specific (Howe and Westley 1988). The bees that visit *F. decumbens* flowers are generalist species and might be replaced by other generalists present in the area. An example of this sort of pollinator replacement was reported by Cox (1983). He found that the Hawaiian ieie vine (*Freycinetia arborea* Gaud.) used to be pollinated by several endemic bird species. Extinction or a greatly reduced population size of these species, following European colonization of the islands, resulted in their replacement as pollinators by another bird species, the introduced Japanese white-eye (*Zosterops japonica*).

However, the most prudent approach to conservation of *F. decumbens* would be to preserve and manage not solely *F. decumbens* but as many components of its ecosystem as possible. This would likely include the pollinators, seed dispersers, and other organisms that perform important roles in the plant's life cycle. This ecosystem approach is currently recognized by planners in El Dorado County, who are attempting a community-level approach to conservation in response to very high development pressures (Dennis 1994). The results reported here show the importance of this approach to conservation of *F. decumbens,* as the native pollinator fauna appears to play a critical role in successful sexual reproduction of this rare plant species.

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ANNOUNCEMENT

The Shrub Research Consortium in concert with New Mexico State University is sponsoring the Ninth Wildland Shrub Symposium, May 23–25, 1995 at the Hilton Hotel in Las Cruces, New Mexico. The symposium theme is "Shrubland Ecosystem Dynamics in a Changing Environment." There will be a mid-symposium field trip to the Jornada Experimental Range/Long Term Ecological Site. Contributed papers are invited. The proceedings will be published by the USDA Forest Service, Intermountain Research Station. If you would like to present a paper, send a title and abstract by September 15, 1994 to Dr. Jerry Barrow, Jornada Experimental Range, Box 30003, Dept. 3JER, New Mexico State University, Las Cruces, New Mexico 88003-8003. To receive preregistration materials and information please contact: Katie Dunford, Office of Conference Services, Box 30004, Dept. CCSU, New Mexico State University, Las Cruces, New Mexico 88003-8004.

WATER USE STRATEGIES OF FIVE SYMPATRIC SPECIES OF *QUERCUS* IN CENTRAL COASTAL CALIFORNIA

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ABSTRACT

We examined the late summer predawn and midday xylem water potential of 247 trees of five *Quercus* species at the Hastings Reservation in central coastal California. These five species are sympatric over a large part of their range in California, but show markedly different strategies in water acquisition and use. *Quercus douglasii* and *Q. kelloggii*, two deciduous species, had the lowest daytime xylem water potentials and the highest recovery values, indicating considerable drought tolerance. *Quercus lobata*, a third deciduous species, had consistently high predawn values, indicating access to ground water and hence the greatest drought avoidance. The two evergreen species, *Q. agrifolia* and *Q. chrysolepis*, had the lowest recovery values, consistent with shifting part of their growth to the winter as part of a drought evading strategy. Correlations between xylem water potential and tree size (DBH) were positive for *Q. agrifolia* but otherwise weak. Elevational effects were significant for several species but did not consistently correlate with elevational preferences. Topographic correlates of water availability as they are usually envisioned did not predict water stress as indicated by xylem water potential. Water relations help explain the distributional differences of these species. *Quercus lobata* consistently taps the water table on alluvial terraces where the water table is too low for other species, such as *Q. agrifolia*, to reach. *Quercus agrifolia* is able to grow in drier environments than *Q. lobata*. *Quercus chrysolepis* is similar to *Q. agrifolia*. *Quercus douglasii* and *Q. kelloggii* are highly drought tolerant and able to grow in dry soils.

The climate in much of California is characterized by wet winters and dry summers. This pattern severely limits plant growth (Hanes 1965). Plants exhibit three general strategies for dealing with the problems associated with such climates: (1) Drought avoidance—Avoidance of desiccation, for example by improved water uptake, water reservoirs or a reduction of transpiring surfaces (Larcher 1980); (2) Drought tolerance—Physical and physiological modifications allowing plants to tolerate extremely dry conditions; (3) Drought evading—A shift in the growing season to the wetter but colder periods of the year (Larcher 1980).

[1] Present address: Hastings Natural History Reservation, 38601 E. Carmel Valley Road, Carmel Valley, California 93924.

Oaks dominate the vegetation over a large part of California, often with several species occurring sympatrically (Cooper 1922; Griffin 1977; Sawyer et al. 1977). Within a given vegetation type, species are often spatially separated. Several authors have related this to soil water availability. Cooper (1926), for example, remarked that *Q. agrifolia* grows mainly close to streams and has a superficial root system while *Q. lobata* has a well developed tap root, capable of exploiting deep-seated water.

We measured the xylem water potential of 247 trees of five California *Quercus* species at Hastings Reservation in central coastal California with the goal of understanding the adaptations they exhibit to cope with the rigors of a Mediterranean climate and the way that these adaptations allow closely related species to coexist. By measuring xylem water potential in late summer both at predawn, when trees have fully rehydrated, and during the day, when water stress is at its maximum, we made three measurements of water relations: (1) Daytime xylem water potential (DAY)—A low value indicates drought tolerance and ability to cope with dry conditions; (2) Nighttime, predawn xylem water potential (PREDAWN)—A high value indicates that the tree has considerable water resources available to it, most likely by being rooted to deep-seated ground water; (3) Overnight recovery (RECOVERY)—This value is the difference between (2) and (1). A low overnight recovery indicates that rehydration is limited, resulting in lower stomatal conductance (Waring et al. 1981). Because there is a direct relationship between water loss and photosynthesis (Farquhar and Sharkey 1982), photosynthesis is potentially limited by this lack of rehydration. Individuals exhibiting low overnight recovery are most likely shifting part of their growth to other seasons, as has been documented for *Q. agrifolia* relative to *Q. lobata* (Hollinger 1992). Low recovery consequently suggests drought evasion.

STUDY SITE AND METHODS

Study site. The study was conducted at Hastings Natural History Reservation, Monterey County, located in the northern Santa Lucia Mountains of central coastal California (36°23'N, 121°33'W) approximately 20 km east of the Pacific Ocean at an elevation of 500 to 900 m. The climate is Mediterranean with a mean annual rainfall of 540 mm (range 261 to 1112 mm), over 90% of which falls from November to April. The mean minimum temperature varies from 1.4°C in January to 9.7°C in August, the mean maximum from 15.6°C in January to 30.4°C in July.

Hastings Reservation is situated in the middle of the central coast range, which stretches from San Francisco to Santa Barbara. The vegetation consists of a patchwork of chaparral, valley grasslands,

TABLE 1. NAMES AND CHARACTERISTICS OF OAKS USED IN THIS STUDY. Values are for trees sampled at Hastings Reservation and are compared with Kruskal-Wallis 1-way ANOVAs (df = 4); values are means ± SD (coefficient of variation). Mean aspect excludes trees growing on level slopes; value presented is calculated using circular statistics. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Species					χ^2
	Q. lobata	Q. douglasii	Q. chrysolepis	Q. agrifolia	Q. kelloggii	
Subgenus	Quercus ("white")	Quercus ("white")	Protobalanus ("intermediate")	Erythrobalanus ("black")	Erythrobalanus ("black")	
Deciduous?	Yes	Yes	No	No	Yes	
n trees	87	56	21	63	20	
DBH (cm)	80.6 ± 33.8	64.2 ± 24.7	50.8 ± 27.3	76.2 ± 29.4	82.0 ± 36.0	24.0***
Stems	1.05 ± 0.30	1.04 ± 0.26	2.57 ± 2.20	1.29 ± 0.68	1.00 ± 0.00	59.4***
Basal area (cm²)	6069 ± 4975	3729 ± 2901	3725 ± 3105	5778 ± 4667	6250 ± 4694	15.2**
Elevation (m)	620 ± 140	633 ± 120	654 ± 173	556 ± 111	773 ± 107	33.4***
Slope (degrees)	9.5 ± 8.5	16.9 ± 8.6	9.3 ± 9.5	8.4 ± 9.1	15.3 ± 8.2	36.8***
Aspect (degrees)	47	120	68	62	0	
Xylem water potential (MPa)						
Day	-2.38 ± 0.49 (20.6)	-3.42 ± 0.61 (17.8)	-2.47 ± 0.56 (22.7)	-2.09 ± 0.49 (23.4)	-3.46 ± 0.36 (10.4)	122.6***
Predawn	-0.72 ± 0.30 (41.7)	-1.53 ± 0.56 (36.6)	-1.84 ± 0.64 (34.8)	-1.22 ± 0.58 (47.5)	-1.53 ± 0.42 (27.4)	110.9***
Recovery	1.66 ± 0.55 (33.1)	1.89 ± 0.63 (33.3)	0.64 ± 0.49 (76.6)	0.87 ± 0.36 (41.4)	1.93 ± 0.52 (26.9)	115.3***

coastal sage brush, riparian, mixed evergreen forest and oak wood-
lands. Tree density varies greatly, from open grasslands and savan-
nas with only occasional scattered individuals to mixed hardwood
forests with nearly closed canopies (White 1966a, b; Griffin 1971).

Study species. We studied 5 species, all common in the study site
(summary information on the taxonomic status of the species is
presented in Table 1). Except where noted, distributional informa-
tion is from Griffin and Critchfield (1972), Munz and Keck (1968),
and Hickman (1993).

(1) *Quercus lobata* Nee—The valley oak is a winter-deciduous
species, endemic to California, and occurs mostly in valleys, fertile
alluvial terraces, on gentle slopes in foothill woodland and riparian
forests from 600 m to 1700 m. It is consistently reported as having
a deep root system connected to ground water (Griffin 1973).

(2) *Quercus douglasii* Hook. & Arn.—The blue oak is one of the
more xerophytic of California oaks (Cooper 1922) and its growth,
measured as basal area increment, is reported to have a high cor-
relation with precipitation (Kertis et al. 1993). It is another winter-
deciduous species endemic to and widely distributed in California,
dominating part of the foothill woodlands on dry, rocky slopes below
1200 m (Baker et al. 1981). This species has previously been found
to vary considerably in the degree to which individuals are rooted
to the water table (Callaway et al. 1991).

(3) *Quercus chrysolepis* Liebm.—The canyon live oak is an ev-
ergreen species and is the most widely distributed oak in California,
with a range from Oregon in the north to Baja California in the
south. It is common on steep, rocky canyon slopes from 200 m to
2600 m.

(4) *Quercus agrifolia* Nee—The coast live oak is an evergreen
species occurring commonly in valleys and on relative wet slopes in
both foothill woodland and in mixed evergreen woodland below
1000 m in the northern part of its distribution and up to 1500 m
in the southern part. In contrast to the other four species studied
here, it is widely distributed along the coast. Canon (1914a, b) re-
ported that this species has an extensive shallow root system. More
recently, Griffin (1973) showed that some *Q. agrifolia* are connected
to the ground water table.

(5) *Quercus kelloggii* Newb.—The California black oak is a winter
deciduous species widely distributed in upland and montane areas
mostly from 300 to 2500 m. Little information on the rooting habit
has been reported for this species; it is thought to have a single major
tap root or numerous major vertical roots (Rundel 1979).

Methods. We measured daytime (DAY) and night-time predawn
(PREDAWN) xylem water potential of 87 *Q. lobata,* 56 *Q. douglasii,*
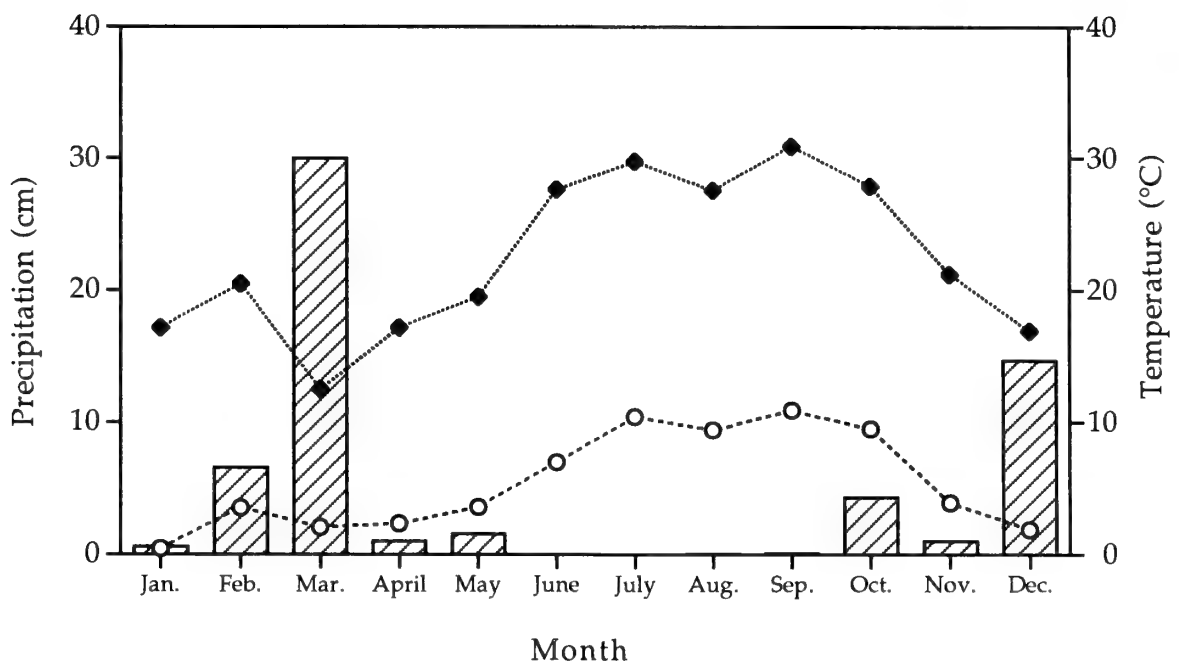
FIG. 1.   Precipitation (▨), average monthly maximum (◆) and minimum temperature (O) at Hastings Natural History Reservation during 1991.

63 *Q. agrifolia,* 20 *Q. kelloggii* and 21 *Q. chrysolepis.* Trees were distributed throughout Hastings Reservation over a distance of approximately 3.5 km and were initially chosen in 1980 as part of an ongoing study of acorn production (Koenig et al. 1994). Trees selected were generally large, mature individuals.

Xylem water potential (Ψ) was measured using the pressure chamber technique (Waring and Cleary 1967; Ritchie and Hinckley 1975). Trees were measured with a pressure bomb (PMS Instrument Co.) from 20 September to 5 October 1991. Daytime measurements were made between 1300 and 1700 while nighttime measurements on the same trees were made on the subsequent night between 0200 and 0600. Short shoots, approximately 5–10 cm long with a minimum of 3 leaves were cut from which xylem water potential was immediately measured in the field. We measured 2 shoots per tree; if the difference between them was more than 10%, we measured a third twig. All daytime twigs were cut from branches located in full sunlight.

The study was conducted at the end of the dry season when temperatures are hottest and water stress the greatest (Fig. 1). Furthermore, 1991 followed 5 years of below average rainfall (1 July–30 June seasonal rainfall ranged from 265 mm to 471 mm from 1986–1987 to 1990–1991, 69 to 275 mm below average). Thus, although only a single set of measurements was made on each tree, the values are likely to represent maximum water stress for individuals in this sample.

Percent of total
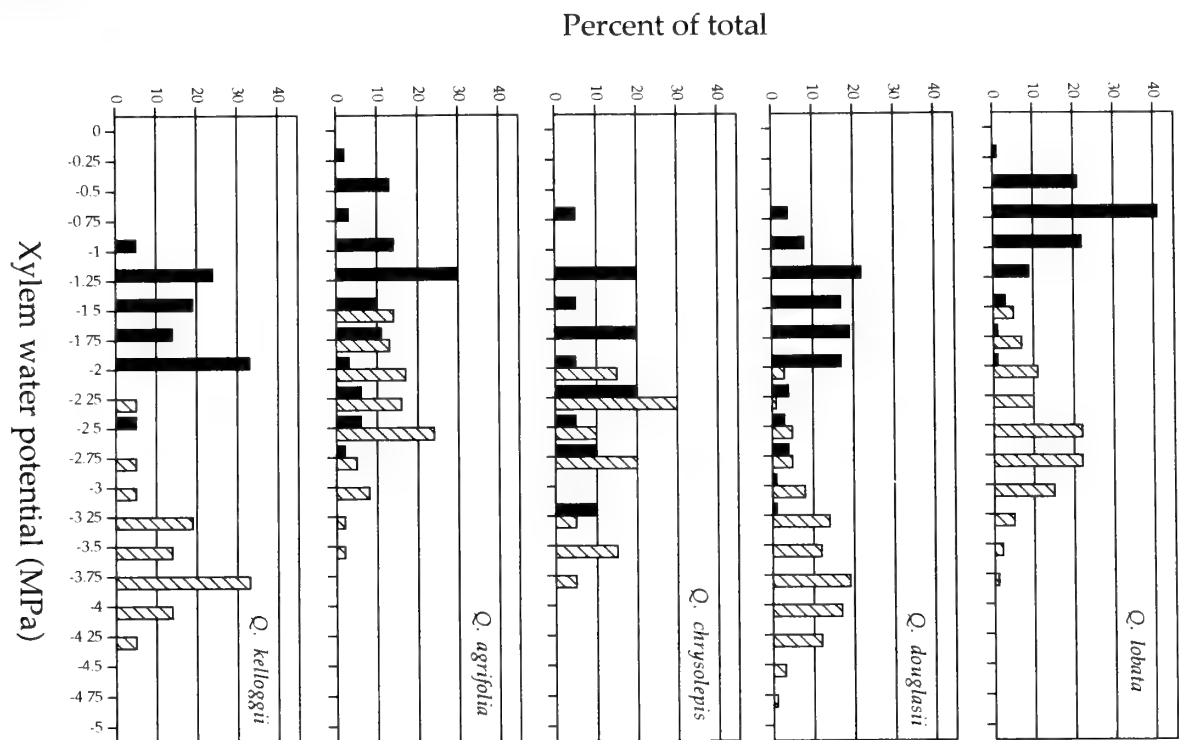
FIG. 2.   Predawn and midday xylem water potential (in MPa). ■ predawn values; ▨ daytime values.

RESULTS

Characteristics of trees. The number of stems, the mean size measured of the biggest stem (DBH), the basal area of all stems and elevation of the sampled trees are listed in Table 1. The three deciduous oak species have, in general, one main stem, whereas *Q. agrifolia* and *Q. chrysolepis* have often more than one main stem. Overlap in both size and elevation was extensive for all of the species, as we used similar criteria to initially choose them and we sampled each over the same elevational gradient. However, on average, *Q. douglasii* and *Q. chrysolepis* individuals were smallest and *Q. agrifolia* located at the lowest elevation. *Quercus douglasii* and *Q. kelloggii* individuals tended to be found on steeper slopes than the other three species (Table 1).

Species differed highly significantly from one another in all three measures of xylem water potential (Table 1, Figs. 2, 3). *Quercus kelloggii* and *Q. douglasii* were almost identical with the lowest DAY and the highest RECOVERY values. Mean DAY values were roughly equivalent for the other 3 species, which instead differed greatly in both their PREDAWN and RECOVERY values, with the live oaks (*Q. chrysolepis* and *Q. agrifolia*) having low PREDAWN and low RECOVERY and *Q. lobata* having high PREDAWN and high RECOVERY. The coefficient of variation of the PREDAWN values

Percent of total
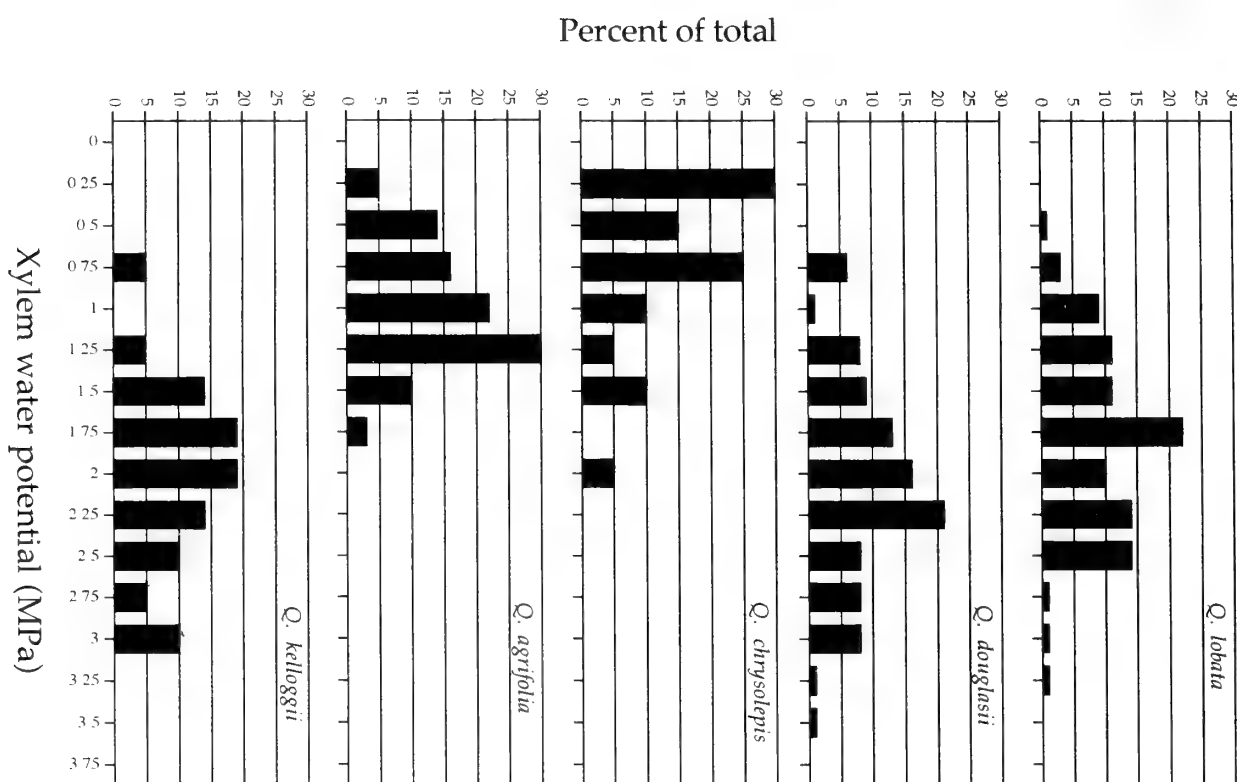
Fig. 3. Recovery of xylem water potential (predawn minus midday values, in MPa).

was twice that of the DAY values, indicating that individuals within each species differ more in their access to water than in tolerance for dehydration. The distributions of Ψ values were not significantly different from normal (15 Kolmogorov-Smirnov 1-sample tests [3 per species], all $P > 0.05$).

Intraspecific correlations of xylem water potential. Table 2 lists Spearman rank correlations of Ψ values with themselves (DAY with PREDAWN) and with DBH, basal area and 2 site characteristics (elevation and slope). Correlations were diverse across the 5 species for all variables. For example, DAY and PREDAWN values were significantly correlated in *Q. douglasii, Q. chrysolepis,* and *Q. agrifolia,* but not for either *Q. lobata* or *Q. kelloggii;* elevation and PREDAWN values were positively correlated in *Q. agrifolia* but inversely correlated in *Q. lobata.*

Aspect was tested by comparing mean Ψ values for trees with north, east, south, and west aspects using a Kruskal-Wallis 1-way ANOVA. No significant correlations between aspect and Ψ were found for *Q. agrifolia, Q. chrysolepis,* or *Q. kelloggii.* Values for *Q. lobata* and *Q. douglasii* are presented in Table 3. Values were significantly different for PREDAWN (both species) and DAY (*Q. douglasii* only), but differences were not readily interpretable. For *Q. lobata,* north-facing trees had the lowest night values, while for *Q. douglasii,* west-facing trees had the lowest DAY and PREDAWN

TABLE 2. SPEARMAN RANK CORRELATIONS BETWEEN XYLEM WATER POTENTIAL AND TREE/SITE CHARACTERISTICS. * = P < 0.05; ** = P < 0.01; *** = P < 0.001 (2-tailed).

	Q. lobata	Q. douglasii	Q. chrysolepis	Q. agrifolia	Q. kelloggi
DAY with					
PREDAWN	0.05	0.42**	0.69***	0.76***	0.05
DAY with					
DBH	−0.04	−0.07	0.40	0.40**	0.15
Basal area	−0.02	−0.07	0.41	0.30*	0.15
Elevation	−0.19	−0.44***	0.64**	0.28*	0.13
Slope	0.06	0.06	0.43	−0.04	0.45*
PREDAWN with					
DBH	0.05	0.06	0.28	0.43***	0.15
Basal area	0.03	0.08	0.29	0.40**	0.15
Elevation	−0.50***	0.13	0.43	0.34**	0.22
Slope	−0.46***	−0.35**	0.42	0.04	−0.33
RECOVERY with					
DBH	0.10	0.09	0.06	0.16	0.09
Basal area	0.08	0.11	0.01	0.28*	0.09
Elevation	−0.07	0.47***	−0.19	0.15	−0.11
Slope	−0.22*	−0.32*	0.06	0.16	−0.64**

values. There were no significant differences in RECOVERY among trees with different aspect.

DISCUSSION

Intraspecific variation. Correlations between site characteristics (elevation, slope, and aspect) and Ψ values were variable and, as previously noted by Griffin (1973), not generally correlated with moisture gradients as they are usually envisioned. For example, water stress should increase with slope, because the redistribution of rainwater through run-off and soil water by saturated throughflow depends on the slope inclination (Band et al. 1993). As expected

TABLE 3. EFFECT OF ASPECT (DIVIDED INTO CARDINAL DIRECTIONS) ON XYLEM WATER POTENTIAL OF *Q. LOBATA* AND *Q. DOUGLASII*. Statistical tests are by Kruskal-Wallis 1-way ANOVA; * = P < 0.05.

	Q. lobata				Q. douglasii			
	Day	Night	Recovery	n	Day	Night	Recovery	n
North	−2.41	−1.00	1.41	16	−3.68	−1.45	2.23	5
East	−2.45	−0.79	1.66	23	−3.43	−1.60	1.83	27
South	−2.54	−0.64	1.89	6	−3.13	−1.10	2.02	12
West	−2.28	−0.70	1.58	15	−3.74	−1.77	1.97	10
χ^2 (df = 3)	1.4	8.9*	4.1	—	8.1*	10.8*	1.8	—

from this assumption, the three deciduous species (*Q. lobata, Q. douglasii,* and *Q. kelloggii*) all had lower PREDAWN and RECOVERY values with increasing slope (Table 2). However, relationships between slope and both PREDAWN and RECOVERY were positive and nonsignificant for the two evergreen species. We would also predict water stress to be greatest for trees on slopes with a south-facing aspect. In general, there was either no significant relationship between Ψ values and aspect or the relationship did not follow this a priori prediction: for neither *Q. lobata* or *Q. douglasii* were the lowest PREDAWN or RECOVER values found in individuals on south-facing slopes (Table 3).

Griffin (1973) also found evidence of size-class effects, with smaller trees showing lower Ψ values than larger trees. Our results provide at best weak support for this relationship: DBH or basal area were positively and significantly correlated with DAY, PREDAWN and RECOVERY values for only 1 of the species (*Q. agrifolia*). However, in general we used mature trees; size-class effects may be stronger among younger age classes.

Previously, Callaway et al. (1991) divided *Q. douglasii* at Hastings Reservation into "positive" and "negative" trees based on their PREDAWN values and presumed degree of rooting to the water table. Our data indicate that this categorization is incomplete. The distribution of *Q. douglasii* Ψ values was normally distributed, suggesting that there is a continuum in xylem water potentials for individuals of this species. Also, individual variation in Ψ values among *Q. douglasii* were comparable to that observed within the other four species.

Interspecific variation. Water relations of the five species were distinctly different. *Quercus kelloggii* and *Q. douglasii* demonstrated the greatest drought tolerance as indicated by low DAY and high RECOVERY values (Table 1, Figs. 2, 3). These species were also found on the steepest slopes. *Quercus lobata* showed the highest PREDAWN values probably caused by the use of deep-seated ground water, while *Q. chrysolepis* had the lowest PREDAWN xylem water potential. Species exhibiting the greatest degree of drought evasion as indicated by low RECOVERY values were the live oaks *Q. chrysolepis* and *Q. agrifolia.*

Based on these results the five species can be divided among the categories for coping with dry conditions listed in the introduction (Table 4). *Quercus lobata* exhibits drought avoidance by tapping into and using deep-seated ground water. *Quercus douglasii* and *Q. kelloggii* are the most drought tolerant as indicated by their relatively low DAY values (Scholander et al. 1965; Waring and Schlesinger 1985). The evergreen species, *Q. chrysolepis* and *Q. agrifolia,* are not particularly drought tolerant as expressed by relatively high DAY

TABLE 4. DROUGHT ADAPTATIONS OF CENTRAL COASTAL CALIFORNIA OAK SPECIES INFERRED FROM XYLEM WATER POTENTIAL PATTERNS.

	Elevation	
	Low	High
Drought avoidance	*Q. lobata*	*Q. lobata*
Drought tolerance	*Q. douglasii*	*Q. kelloggii*
Drought evading	*Q. agrifolia*	*Q. chrysolepis*

values and do not appear to tap the ground water to a large extent; growth by these species is limited during the extensive dry season. Instead, these species are drought evasive, shifting part of their growth cycle into the colder part of the year.

Water relations and oak distribution. As noted by prior workers, *Q. lobata* consistently taps the ground water on alluvial terraces where the water table is too low for *Q. agrifolia* to reach. The drought evading *Quercus agrifolia* is better able to grow in canyons and riparian forests as well as in coastal areas where it exploits relatively mesic areas with longer water availability. In addition, *Q. agrifolia* is more shade tolerant (Cannon 1914a, b; Callaway 1992) and is able to form a dense shade and thus has an advantage in low water and nutrient environments over *Q. lobata* (Cooper 1926; Hollinger 1992). *Quercus chrysolepis* appears to function similarly but at generally higher elevations. *Quercus douglasii* and *Q. kelloggii* are the two most drought tolerant species occupying dry slopes and ridges (Griffin and Critchfield 1972), with soils able to supply enough water in the summer.

Distributional preferences of the species were only partially reflected by the correlations between Ψ values and elevation (Table 2). For example, as expected from the generally lower elevational distribution of *Q. douglasii* and higher distribution of *Q. chrysolepis*, DAY values correlated negatively with elevation in the former species and positively with elevation in the latter. However, there was no correlation between Ψ values and elevation in *Q. kelloggii* despite its preference for higher elevations, and there was a positive relationship between DAY values and elevation for *Q. agrifolia*, even though this species prefers lower elevations and is the only one of the five found at sea level in central coastal California.

Our results confirm that trees employing several contrasting water use strategies can coexist within a site. Sympatric oak species segregate by differences in water use depending primarily on the amount of water available in the summer and secondarily on the timing of the main growing season. These differences in water exploitation and drought adaptations probably have major effects on the distribution

(Terradas and Savé 1992) and coexistence (Hall and McPherson 1980) of oaks on a microgeographical scale and, most likely, on a macrogeographical scale as well, thereby contributing to the mosaic of vegetation types dominated by one or more oak species characterizing much of California.

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DYNAMICS OF *QUERCUS WISLIZENII* FOREST AND SHRUBLAND IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA

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Abstract

Vegetation dominated by *Quercus wislizenii* (interior live oak) in the San Bernardino Mountains may be classified as chaparral or hardwood forest, depending on its structure and composition. Structure, dynamics, and species composition are described differently for *Q. wislizenii* forest and chaparral, but relationships among these types are not always clear. This leads to uncertainty in classification and management. We sampled *Q. wislizenii* stands in the San Bernardino Mountains, then used multivariate techniques to group plots and to distinguish among characteristics of *Q. wislizenii*-dominated chaparral and forest. We identified and described one forest type and two distinct shrubland types. We conclude that one of the shrubland types, occurring with sprouting chaparral species on steep mountain sides, is best recognized as interior live oak chaparral. The other type, occurring on more moderate slopes, is better considered an early-developmental interior live oak forest. About half of the sample plots remained unclassified, indicating floristic and structural continua rather than discrete categories. Structural and floristic characteristics of the three types are used to clarify relationships between *Q. wislizenii* chaparral and forest, and to describe development of forest from shrublands that resemble chaparral. We recommend consideration of these relationships in management decisions.

The intent of vegetation classification is to document repeating patterns in natural vegetation. Unlike biological taxa, species assemblages do not share genetic heritage, and vegetation ecologists do not expect every stand to correspond unambiguously to a single described type. Nevertheless, management policies often differ according to vegetation (e.g., San Bernardino National Forest 1988), and therefore rely on correct identification of vegetation types.

Quercus wislizenii A. DC. (interior live oak) occurs in forest and shrubland throughout cismontane California. Stands dominated by this species may be classified as either forest or chaparral, depending on canopy height, density, and on understory composition. Conversely, *Q. wislizenii* shrubland and forest might be seen as structural or developmental phases of a single vegetation type. We examined

Q. wislizenii stands in the San Bernardino Mountains to determine (1) whether important floristic or structural differences could be used to distinguish *Q. wislizenii* chaparral and forest, and (2) whether chaparral and forest are best recognized as distinct types or as developmental phases of a single type.

Quercus wislizenii occurs throughout much of California and in northern Baja California. A shrubby variety, *Q. wislizenii* var. *frutescens* Engelm., is evidently sympatric with *Q. wislizenii* var. *wislizenii* throughout much of its range (Tucker 1993). We did not attempt to distinguish between varieties in this work. *Quercus wislizenii* occurs as a dominant component in many vegetation types. Allen et al. (1989) described six interior live oak associations in the Sierra Nevada and Coast Ranges, including associations with hardwood trees (*Arbutus menziesii, Quercus douglasii*), a conifer (*Pinus sabiniana*), shrubs and subshrubs (*Arctostaphylos, Rhamnus, Heteromeles arbutifolia, Toxicodendron diversilobum, Eriodictyon californicum, Ceanothus cuneatus*), grasses, and herbs. Barbour (1988) included it as a characteristic species in a "nonconiferous phase" of cismontane California mixed evergreen forest. Patric and Hanes (1964) described a mature forest stand in the San Gabriel Mountains dominated by *Q. wislizenii*. Holland (1986) implied a developmental relationship between *Q. wislizenii* forest and chaparral. He described interior live oak chaparral as a distinct type, similar to forest, but prone to more frequent fire, calling it a "fire disclimax." Interior live oak forest, in Holland's description, is "not a fire type" but may burn periodically and resembles chaparral after fire. He noted that *Q. wislizenii* resprouts vigorously and "recovers rapidly after fire."

Minnich (1976) described vegetation of the San Bernardino Mountains. Two of his types, "mixed chaparral" and "oak chaparral," sometimes include *Q. wislizenii* as a dominant or important species. Obligate sprouting shrubs (Keeley 1986) are predominant in both types, and both types correspond roughly to Hanes' (1977) description of chaparral on north-facing slopes. Minnich also described an "oak woodland," dominated by *Q. chrysolepis*, with a "solid umbrella-like canopy" and an understory of "patches of winter annuals in openings and small shade-tolerant shrubs, including *Rhamnus crocea, Rhus ovata, Ribes malvaceum* and *Toxicodendron diversilobum*." His description matches Holland's (1986) canyon live oak forest, and corresponds to composition and physiognomy of other authors' forest descriptions (Sawyer et al. 1977; Barbour 1988).

Chaparral is described typically as dense evergreen shrubland with a closed canopy about one to six m tall, contiguous nearly to the ground, and without significant understory (Hanes 1977). Hardwood forest is taller (to 15 m), with a closed or open canopy, and with a relatively open structure beneath the canopy (Sawyer et al. 1977;

Barbour 1988). In California, hardwood forest structure typically includes shrubs and perennial herbs in the understory.

Chaparral and forest in southern California are both influenced by periodic fire (Kilgore 1981; Minnich 1988). A fire may kill nearly all above-ground biomass (a stand-replacement fire) or may burn at lower intensity through the understory without incinerating or top killing canopies (a stand-altering fire, or low-intensity surface fire). Chaparral normally burns in the stand-replacement pattern: above-ground vegetation is entirely replaced following fire (e.g., Patric and Hanes 1964; Hanes and Jones 1967). Dominant shrubs regenerate from surviving underground structures (James 1984) or from seed, and stands often redevelop their pre-fire composition within a few years. Forests may undergo either stand-replacement fires or stand-altering fires, depending on stand characteristics and fire conditions. In the San Bernardino Mountains, *Q. wislizenii* stands seem to burn only in the stand-replacement pattern. Canopies usually burn completely but stems are intolerant of fire at their bases and are top-killed by low-intensity surface fire (Plumb 1980). We have seen no evidence of *Q. wislizenii* stems that have survived historic fires.

Most descriptions of chaparral dynamics have indicated little recruitment of new shrubs or herbs after the first few years and little or no understory beneath established shrub canopies. In contrast, mature hardwood forests often have an understory of shade-tolerant saplings which can recruit into the canopy (e.g., McDonald and Littrell 1976). Yet chaparral and hardwood forest dynamics are not so sharply distinct from one another. Structure and development in some chaparral stands, especially those in which obligate sprouting taxa occur, may resemble those of hardwood forests. Hanes (1971) noted open structure beneath the canopy in long-unburned chaparral on north-facing slopes, and Patric and Hanes (1964) found greater species diversity in older north-slope stands, perhaps indicating germination and recruitment of species absent from the post-fire environment. Keeley (1992) showed abundant recruitment of seedlings and asexually-produced stems into long-unburned chaparral canopies. We conclude here that *Q. wislizenii* forests in the San Bernardino Mountains develop from shrublands resembling chaparral, providing further evidence of similarities in structure and function of forest and chaparral.

METHODS

We analyzed 91 *Q. wislizenii* plots, including 75 0.1 ha plots sampled for this report (Fig. 1) and 16 0.04 ha plots provided by the US Forest Service (USFS) from its Southern California Ecosystems Classification project. We sampled stands with at least 30% *Q. wislizenii* cover (estimated from outside the stand; recorded cover was
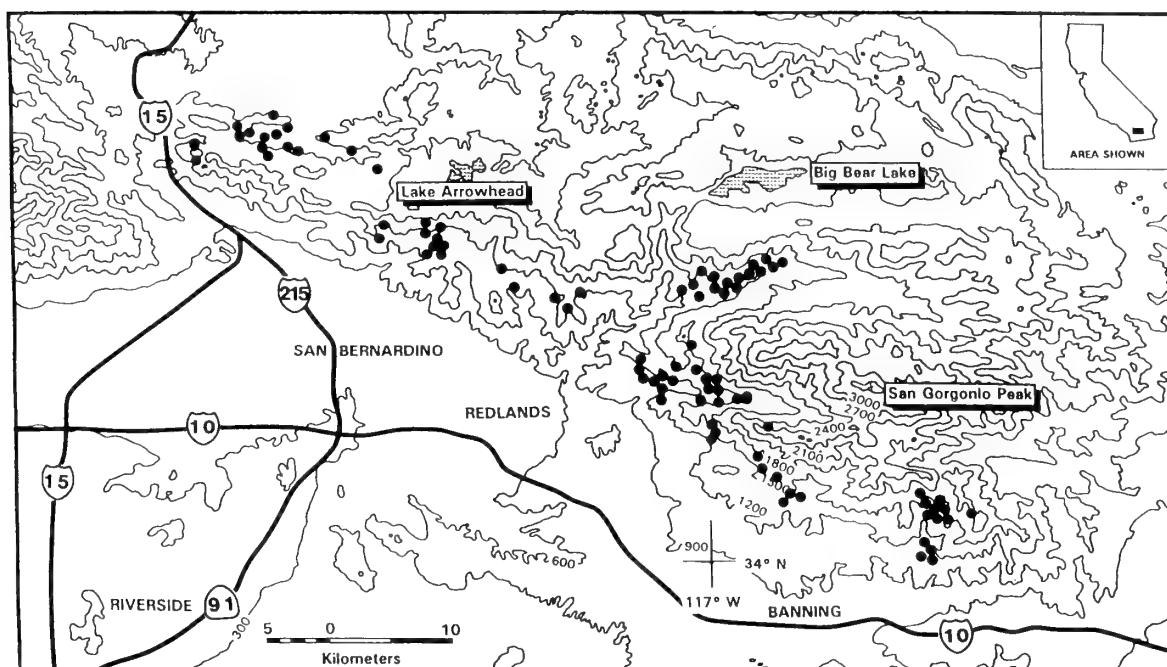
FIG. 1.   Plot locations. Contour lines at 300 m intervals.

sometimes as low as 20%) and without obvious human-associated disturbance (evidence of grazing or woodcutting was found in some plots). Plot locations were chosen subjectively, and sampling was not stratified by vegetation structure or composition. USFS plot locations were originally selected by presence of vegetation structurally resembling chaparral and absence of obvious human-associated disturbances. The 16 USFS plots used here were selected from 190 chaparral plots, based on 20% or greater cover of *Q. wislizenii*, as recorded in the data.

Site characteristic data (location, elevation, slope, aspect) were noted for all plots. Detailed soil descriptions were collected for the USFS plots; in our plots, soil was simply characterized as either alluvial-colluvial or residual. Floristic data included a census of woody plant species with estimated percent cover and average height for each species. Total canopy cover (defined as total cover of all plants sharing the *Q. wislizenii* overstory stratum or emerging above it) was estimated. Seedling and sapling numbers were estimated for each species and recorded separately in our 75 plots; seedlings and saplings were not distinguished from canopy plants in USFS plots. In our plots, total herbaceous cover was estimated visually but cover values were not recorded by species. USFS data included a census of herbaceous plants and estimates of cover values for each species.

In our 75 plots, but not in the USFS plots, basal stem diameters and numbers per *Q. wislizenii* individual (genet) were recorded for 20 oaks in each plot. Genets were not randomly selected, and tended to be grouped at plot centers. Up to five stems were measured for

each selected oak (all stems were measured where five or fewer occurred). Stem diameters were measured near their bases (above basal swellings) using a forester's dbh tape except where stems were inaccessible; these diameters were estimated visually. It was often difficult to judge whether a group of stems represented a single genet or a clonal extension of an adjacent oak because *Q. wislizenii* reproduces asexually from fallen limbs and from below-ground structures. We considered genets to be distinct if their above-ground structures were separated by at least one-half meter from adjacent stems. We did not excavate roots or burls to verify these judgements, and we undoubtedly attributed some stems to wrong genets.

For analyses, stem diameters were arranged into 5 cm interval classes. Plot aspect was converted to its cosine so that slopes with similar solar exposure would have similar values. Shapiro and Wilke's W statistic was used to test data for normality (Engelman 1990a). Univariate analysis of variance, using Welch's separate group t-test, was used to analyze mean slope values among plot catergories (Dixon et al. 1990). Cluster Analysis of Cases (Engelman 1990b), using the sum of squares coefficient of similarity, and K-Means Cluster Analysis of Cases (Engelman and Hardigan 1990), were used to classify plots into categories.

No variables were normally distributed. Most were highly leptokurtic (peaked distribution curve) and skewed to the right. Cosine of plot aspect, percent slope, and *Q. wislizenii* cover were bimodally distributed. Skewed frequency distributions resulted in many small, dissimilar, clusters in cluster analyses of raw floristic data. To generate clusters of related plots, we grouped species according to structural and life history characteristics and treated these groups as new variables (Table 1). *Quercus wislizenii* cover was retained as a separate variable.

Floristic and structural data were analyzed separately with both programs; thus, four independent cluster analyses were used. Forest plots were identified from structural data, and non-forest plots were clustered from floristic data. Plots which remained unclassified by cluster analyses were separated into two categories according to slope, using 30% slope as the breakpoint (the threshold corresponds to the node in percent-slope's bimodal distribution and separates plots on alluvial-colluvial soils almost perfectly from those on residual soils). The two new categories were named "unclassified-moderate" and "unclassified-steep." Stepwise discriminant function analysis (SDF; Jennrich and Sampson 1990) was used to identify variables providing the strongest discrimination between groups identified by cluster analysis. Only those floristic variables with means greater than 1.0 across all groups and occurring in 10 or more plots were used. Where pairs of remaining variables had correlation values of 0.6 or greater, only one member of the pair was retained.

TABLE 1. NUMBER OF OCCURRENCES OF EACH SPECIES IN SAMPLED STANDS. Arranged by stature and life history categories used in cluster analyses. Nomenclature follows Hickman (1993); fire responses follow Conrad (1987). [1] Included because of fire-initiated seed release from serotinous cones (Vogl et al. 1977). [2] Species commonly observed beneath shaded canopies in San Bernardino Mountains.

Species	Occurrences	Species	Occurrences
Subshrubs		*Ceanothus* spp.	
Chrysothamnus nauseosus	4	*C. crassifolius*	2
Eriodictyon trichocalyx	27	*C. greggii*	3
Eriogonum fasciculatum	9	*C. integerrimus*	4
Lupinus excubitus	1	*C. leucodermis*	41
Mimulus aurantiacus	2	**Vines**	
Opuntia basilaris	1	*Clematis lasiantha/*	
O. littoralis	6	*C. pauciflora*	3
O. parryi	1	*Lonicera interrupta*	37
Rhus trilobata	29	*L. subspicata*	9
Salvia apiana	8	*Marah macrocarpus*	10
S. mellifera	1	**Trees**	
Solanum xanti	1	*Abies concolor*	2
Trichostema lanceolatum	2	*Fraxinus velutina*	7
Yucca whipplei	16	*Pinus coulteri*	9
Obligate sprouting shrubs		*P. jeffreyi*	4
Arctostaphylos glandulosa	18	*Platanus racemosa*	2
Cercocarpus betuloides	19	*Prunus virginiana*	4
Garrya flavescens	15	*Quercus chrysolepis*	30
Heteromeles arbutifolia	6	*Q. kelloggii*	5
Prunus ilicifolia	9	*Umbellularia californica*	9
Quercus berberidifolia	33	**Shrub seedlings**	
Rhamnus ilicifolia	18	*Amorpha californica*	2
Sambucus mexicana	5	*Arctostaphylos glauca*	1
Obligate seeding & facultative seeding/sprouting shrubs[1]		*Cercocarpus betuloides*	1
		Garrya flavescens	1
Adenostoma fasciculatum	28	*Prunus ilicifolia*	3
Arctostaphylos glauca	14	*Quercus berberidifolia*	2
A. patula	4	*Rhamnus californica/*	
A. pringlei	2	*R. tomentosus*	15
A. pungens	5	*R. ilicifolia*	5
Fremontodendron californicum	3	*Sambucus mexicana*	1
Ericameria pinifolia	4	*Styrax officinales*	2
E. parishii	2	**Tree seedlings and saplings**	
Pinus attenuata[1]	4	*Acer macrophyllum*	1
Forest understory shrubs[2]		*Fraxinus velutina*	3
		Pinus jeffreyi	1
Amorpha californica	8	*Prunus virginiana*	5
Keckiella cordifolia	12	*Pseudotsuga macrocarpa*	1
K. ternata	17	*Quercus chrysolepis*	9
Rhamnus californica/		*Q. kelloggii*	2
R. tomentosus	23	*Q. wislizenii*	39
Ribes roezlii	2	*Umbellularia californica*	7
Rosa californica	2		
Styrax officinales	5		
Symphoricarpos mollis	2		
Toxicodendron diversi-lobum	7		
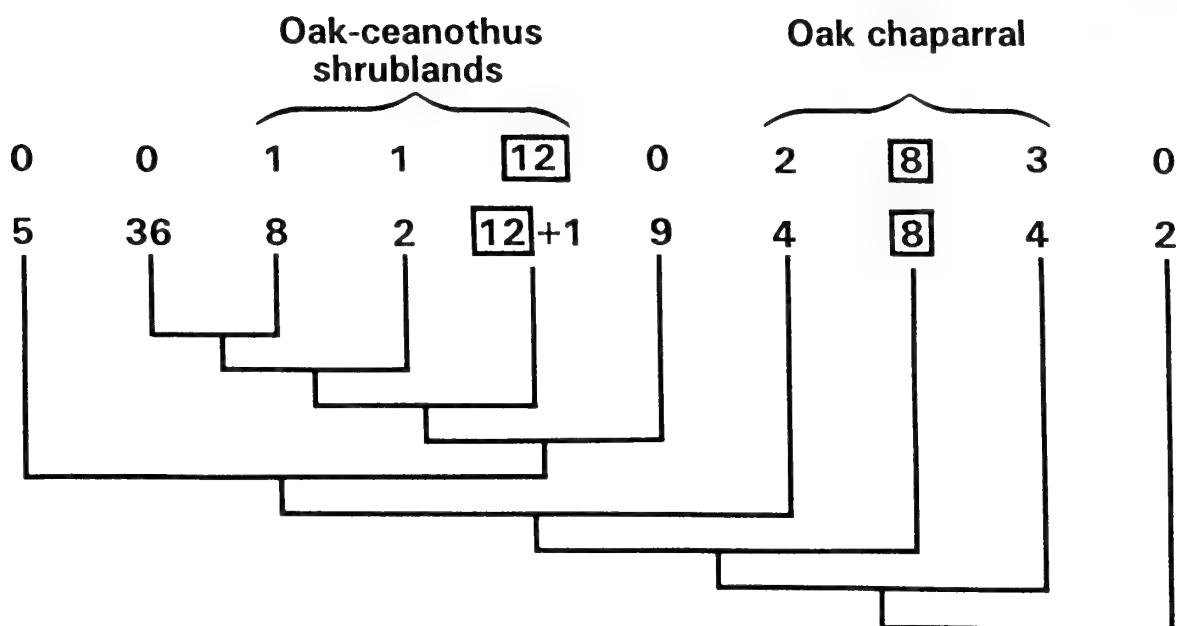
Fig. 2.   Cluster analyses of floristic data (91 plots). Cluster Analysis of Cases (dendrogram) and corresponding selected K-Means clusters (brackets). Boxes indicate agreement by both programs; numbers indicate number of plots per cluster.

Results

Both cluster methods identified two groups of non-forest plots from floristic data, agreeing on classifications of most plots (Fig. 2). Where both programs agreed on a plot's classification, we identified it as either "oak-ceanothus shrubland" (12 plots) or "oak chaparral" (8 plots) based on SDF analysis of floristic variables (below). None of these 20 plots clustered with forest plots in separate analyses of structural data.

Both programs identified two groups of forest plots from structural data, but disagreed on specific groupings. K-means clustering identified two groups with high frequencies in the largest stem size classes, distinguished from one another by frequency differences in smaller size classes. Cluster Analysis of Cases clustered most plots from the K-means groups together but recognized three plots with the largest stems in the data set as a distinct cluster (Fig. 3). Neither program clustered any plots already identified as oak chaparral or oak-ceanothus shrubland with forest plots. Both programs agreed on the classification of 27 plots into clusters characterized by large stem diameters, which we recognized as *Q. wislizenii* forest. Forty-four plots remained unclassified.

Percent slope was the only site variable identified by SDF analysis as useful in discriminating among chaparral, shrubland and forest clusters: forest and oak-ceanothus shrubland groups occur on relatively moderate slopes, while chaparral plots occur on steeper slopes. Unclassified plots occurred on both moderate and steep slopes. Univariate ANOVA found no significant differences among mean slope

Quercus wislizenii
forest plots
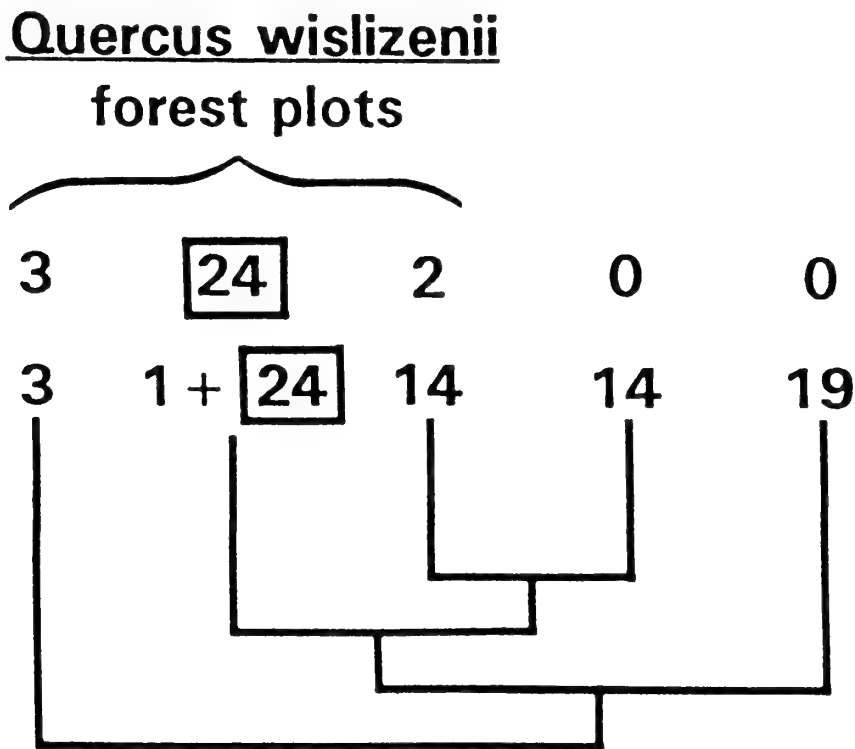
FIG. 3.   Cluster analyses of structure data (75 plots). Cluster Analysis of Cases (dendrogram) and corresponding combined K-Means forest clusters (brackets). Boxes indicate agreement by both programs; numbers indicate number of plots per cluster.

of oak-ceanothus shrubland, *Q. wislizenii* forest, and unclassified-moderate plots at the 95% confidence interval. Similarly, mean slopes of oak chaparral and unclassified-steep plots did not differ significantly. All other comparisons among categories were significant at the 95% confidence level, and most were significant well above the 99% interval.

SDF analysis identified *Ceanothus leucodermis* cover and total obligate sprouting chaparral shrub cover as the floristic variables most useful in discriminating among the five groups. Discriminant models based on these variables identified oak chaparral and oak-ceanothus shrubland with high success, but did not discriminate well between *Q. wislizenii* forest plots and the two unclassified categories. Comparative site, structure and floristic characteristics of the categories are shown in Table 2. SDF analysis identified three structural variables (stem frequency in the 15–20 cm and >20 cm size classes, and *Q. wislizenii* height) which discriminated well between forest plots and other categories. SDF analysis of structural data did not discriminate well between oak-ceanothus shrubland and unclassified groups.

Shrub canopy in chaparral and oak-ceanothus shrubland plots is dense, usually exceeding 80%, and canopy height ranges from 1.3 to 5 m. There is little or no herb cover. Forest understory shrubs (Table 1) occur occasionally but at very low cover in both types. No

TABLE 2. COMPARISON OF OAK CHAPARRAL, OAK-CEANOTHUS SHRUBLAND, INTERIOR LIVE OAK FOREST, AND UNCLASSIFIED CATEGORIES.

Variable	Oak chaparral		Oak-Ceanothus shrubland		Interior live oak forest		Unclassified	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Site characteristics								
Elevation (m)	1486	302	1330	177	1362	168	1345	247
Cos aspect	−0.28	0.69	−0.32	0.88	−0.05	0.68	−0.7	0.8
% slope	45	13	28	18	20	18	39	21
Structure								
Canopy height (m)	3.2	1.3	2.6	1.0	5.9	1.6	4.0	1.6
Total canopy cover (%)	88	5.6	97	2.8	68	18	82	13
Total herb cover (%)	1.2	1.7	0.7	1.0	14	18	5	10
% cover, by category (Table 1)								
Seeding and facultative chaparral shrubs	2.0	3.4	3.2	3.3	1.0	1.5	2	5
Subshrubs	1.8	2.4	3.8	4.8	6	6	4	8
Obligate sprouting shrubs	43	11	3.2	4.2	4	4	5	7
Understory shrubs	0.5	0.8	0.8	1.2	4	6	3	8
Trees	1.9	3.0	0.4	1.0	8	12	2	6
% cover of key species								
Ceanothus leucodermis	11	13	36	18	0.3	0.7	2.0	4
Quercus wislizenii	30	8	52	15	58	17	66	23
Seedling and sapling numbers								
Shrubs	n/a (data avail. for only 2 plots)		0.3	0.7	5	9	5	11
Trees (excluding Quercus wislizenii)			0	—	7	12	0.2	0.7
Quercus wislizenii			0.4	1.3	10	11	1.4	5

shrub or tree seedlings were recorded in oak chaparral plots (data available for only two plots) and seedlings were rare in oak-ceanothus shrubland. No chaparral or shrubland plots have *Q. wislizenni* stems approaching diameters characteristic of forest plots (about 15 cm).

Oak chaparral is distinguished from oak-ceanothus shrubland by its occurrence on residual soils of 30% or greater slope, high cover (30–65%) of sprouting chaparral species (Table 1), and relatively low *Q. wislizenii* cover (20–40%), though these values overlap the ranges of the other types described here.

Oak-ceanothus shrubland occurs primarily on soils of alluvial and colluvial origin on slopes less than 30%. It has low obligate sprouting shrub cover (0–13%) and does not overlap the minimum value in oak chaparral. *Ceanothus leucodermis* cover ranges from 15% to 70%.

Quercus wislizenii forest is defined by structure. Canopy height averages 6 (3–10) m. At least five stems exceeding 15 cm diameter occur in every plot, and most have five or more exceeding 20 cm diameter. *Quercus wislizenii* cover (35–85%) is similar to oak-ceanothus shrubland, and higher than oak chaparral. Average total canopy cover (about 70%) is lower than oak chaparral and oak-ceanothus shrubland. Forest stands have little or no cover of *C. leucodermis,* obligate seeding, or obligate sprouting chaparral shrubs (Table 1). Forest understory species and hardwood trees occur occasionally but none are strongly correlated with forest plots. Forest stands occur primarily on alluvial and colluvial soils with slopes less than 30%, but occasionally much steeper, including one plot on a 90% slope.

Floristically, unclassified groups were not distinguished from forest, but their structure was not distinguished from chaparral and shrubland groups. When unclassified plots were separated into slope categories, slope was the only variable useful in discriminating between the new categories. Unclassified-steep plots and oak chaparral occur on similar steep sites. Unclassified-moderate plots, forest, and shrubland all occur on moderately sloping alluvial-colluvial sites.

DISCUSSION

Distributions of most floristic variables are skewed. Species (other than *Q. wislizenii*) tend to occur in a few plots at high cover, and in many plots at low cover. We believe this reflects distributions of woody plants in the San Bernardino Mountains, rather than sampling bias. The bimodal distributions of slope and aspect probably reflect topography rather than sampling bias. These mountains are steep and are comprised primarily of east-west oriented ridgelines dissected by moderately sloping washes and drainages. Slopes intermediate between moderate drainages and steep mountainsides

are uncommon. *Quercus wislizenii*-dominated stands occur on residual and on alluvial-colluvial soils and on all aspects. *Quercus wislizenii* cover is bimodal, but is not strongly correlated with site or structure variables. Several other species are negatively correlated with high *Q. wislizenii* cover, but there is little correlation among their cover values, and they do not explain the bimodal distribution.

Our descriptions of oak chaparral and oak-ceanothus shrubland are encompassed by Holland's description of interior live oak chaparral (1986); most plots are also encompassed by Minnich's oak chaparral (1976), though some match his mixed chaparral better.

Our description of interior live oak forest compares well to Holland's (1986) description. Most of these stands have the closed canopy and sparse understory resembling *Q. chrysolepis* forests (Minnich 1976, 1980; Holland 1986). A few plots classed here as forest have relatively open canopies, suggesting woodland structure, but they invariably occur on sites influenced by grazing or woodcutting. The association of forest plots with moderate slopes is consistent with Keeler-Wolf's (1990) description of mature *Q. wislizenii* stands on alluvial-colluvial slopes in the southeastern San Bernardino Mountains.

We conclude that chaparral described here matches traditional descriptions of chaparral structure, and we have no evidence that its dynamics differ from other chaparral types dominated by sprouting species. More important, we conclude that oak-ceanothus shrubland, and perhaps unclassified plots on moderate slopes, are early-developmental *Q. wislizenii* forest. They occur on sites indistinguishable in this analysis from forest sites; oaks are shorter and have smaller-diameter stems; and *C. leucodermis,* which dies out of chaparral stands about 40 years after fire (Hanes 1971), occurs as a codominant. We avoid the term "chaparral" for these stands to emphasize the distinction from traditional descriptions of chaparral dynamics. The pattern of interior live oak forest development from a dense oak-ceanothus shrubland parallels Minnich's (1976) description of *Q. chrysolepis* forest development from shrublands with *C. leucodermis* and *C. integerrimus* as codominants.

We classified plots conservatively, assigning plots to categories only when both cluster programs agreed on their classification. This approach is partly responsible for the large number of unclassified plots. But the unclassified plots are also evidence of a continuum between the types described here: shrubland and forest are related through time, while both may be related to chaparral through structure and floristic composition. Some unclassified plots seem to be intermediate between *Q. wislizenii*-dominated vegetation and other types not considered in this analysis (e.g., several plots have high *Q. chrysolepis* cover).

One hypothesis for the predictable occurrence of interior live oak forests on moderate alluvial-colluvial slopes and the contrasting occurrence of oak chaparral on steeper, residual sites presumes that development of mature structure requires relatively long fire intervals. We did not age *Q. wislizenii* stands, but we find strong evidence that interior live oak forest is older and develops over time from oak-ceanothus shrubland. If long fire intervals allow interior live oak forest development, two alternative explanations might argue that *Q. wislizenii* forests should be recognized as long-unburned chaparral.

First, fire may have missed forest-like stands by chance. But the strong correlation of *Q. wislizenii* forest plots with moderate slopes shows that forest distribution is not random. Fire intensity and rate of spread increase with increasing slope (Rothermel 1983). Fire intervals should be shorter on steep slopes than on moderate slopes because ignitions in *Q. wislizenii* stands on steep slopes should establish and spread during a broader range of conditions (e.g., fuel moisture and wind speed) than ignitions on moderate slopes. Stands may also increase their resistance to fire once they reach forest stature, due to vertical fuel arrangement, as Minnich (1980) describes in *Q. chrysolepis* stands. If deep alluvial-colluvial soils allow faster growth than residual soils, then stands on moderate slopes could reach fire-resistant stature at younger ages, further reducing the likelihood that fire will spread through them.

Second, mature *Q. wislizenii* stands may be an artifact of modern fire suppression. Fire intervals and burning patterns in southern California have been altered from a combination of lightning-caused and anthropogenic fires without suppression, to today's pattern dominated by anthropogenic fire with effective suppression of most ignitions (Minnich 1988). Pre-European fire intervals in California are unknown. Present-day human impacts to fire frequency and behavior are complex, involving new ignition sources, suppression of natural ignitions, timing of ignitions (lightning usually occurs during rain or high humidity while human-caused ignitions may occur at any time) and introduction of non-native herbs (e.g., *Bromus*) which ignite and carry fire more readily than native shrubs (D'Antonio and Vitousek 1992). Interaction of human influences with natural fuel characteristics confounds comparison of present-day and historic burning patterns. We cannot reject the hypothesis that *Q. wislizenii* forest is an artifact of fire management, but we find no evidence in its support.

We recommend that land managers in the San Bernardino Mountains recognize distinct *Q. wislizenii* types in policy planning and application. In fire management planning and prescribed burn planning, long fire intervals should be recognized as a normal pattern in

interior live oak forests. Where management directs conversion of chaparral to other vegetation types (e.g., non-native grassland fuelbreaks or conifer plantations), then oak-ceanothus shrubland should be distinguished from chaparral and managed accordingly. Where policy directs management for increased wildlife habitat value, then the forest characteristics of *Q. wislizenii* stands should be recognized (e.g., arboreal nesting habitat, availability of shaded cover, production of acorn mast and basal shoots). Interior live oak forest and oak-ceanothus shrublands should not be managed as chaparral.

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HABITAT CORRELATES AND DISTRIBUTION OF *CORDYLANTHUS MARITIMUS* (SCROPHULARIACEAE) ON TOMALES BAY, CALIFORNIA

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ABSTRACT

A study of 35 colonies of *Cordylanthus maritimus* subsp. *palustris* in salt marshes of Tomales Bay, California, revealed habitat relationships, including patterns of co-occurrence and cover values of associated species, and examined the possible effects of spatial distibution on the occasional failure of annual colonies to appear. The presence of hemiparasitic *C. m.* subsp. *palustris* was strongly associated with the presence of *Triglochin concinna* and *Limonium californicum*. Covariance of cover values within a large colony of *C. m.* subsp. *palustris* corroborated the survey results for *T. concinna*, but was inconclusive for *L. californicum*. Increased species richness and decreased vegetation height were also valuable predictors of greater *C. m.* subsp. *palustris* cover. A three-year investigation of biogeographic relationships suggested that annual probability of a colony to appear was influenced predominantly by patch size and *C. m.* subsp. *palustris* density rather than by sizes or distances of other nearby colonies or populations. We speculate that this reflects very low probabilities of seed dispersal among *C. m.* subsp. *palustris* colonies.

Cordylanthus maritimus Benth. subsp. *palustris* (Behr) Chuang and Heckard, Point Reyes bird's beak, is an annual salt marsh species that occurs along the Pacific coast from Marin County, California, northward to southern Oregon (Chuang and Heckard 1993). It is considered rare throughout its range, and is threatened by loss of coastal salt marsh habitat but is not state or federally listed as threatened or endangered (Skinner and Pavlik 1994). The southern California subspecies, *C. m.* subsp. *maritimus,* salt marsh bird's beak, is state and federally listed as endangered (U.S. Fish and Wildlife Service 1985; Skinner and Pavlik 1994).

Cordylanthus m. subsp. *maritimus* requires a sparse plant canopy that provides high light penetration for seedling survival (Dunn 1987; Fink and Zedler 1989), adjacent upland vegetation that provides suitable habitat for appropriate insect pollinators (Lincoln 1985), reduced tidal inundation (Fink and Zedler 1990), and possibly, low salinities (<8 ppt) for germination (Dunn 1987). These requirements generally limit the occurrence of *C. m.* subsp. *maritimus* to the upper terraces and edges of salt marshes where such conditions may occur (Dunn 1987; Zedler et al. 1992). *Cordylanthus m.* subsp. *palustris* appears to be limited to similar high marsh habitat on Tomales Bay.

TABLE 1.   UNIVARIATE ASSOCIATIONS BETWEEN *CORDYLANTHUS MARITIMUS* SUBSP. *PALUSTRIS* AND OTHER PLANT SPECIES IN SALT MARSHES ON TOMALES BAY, CALIFORNIA. * P < 0.05, ** P < 0.01, *** P < 0.001. [a] Log-likelihood ratio test of association between presence/absence of *C. m.* subsp. *palustris* and presence/absence of other species.

Species/variable	*C. m.* subsp. *palustris* at Walker Creek Delta (product-moment correlation) Percent cover (n = 87)	*C. m.* subsp. *palustris* on Tomales Bay (proportion of sites sampled)		
		Present (n = 35)	Absent (n = 22)	Likelihood ratio test[a]
Atriplex triangularis		0.06	0.50	7.69**
Distichlis spicata	−0.068	1.00	0.82	1.96
Frankenia salina	0.080	0.60	0.45	0.58
Grindelia hirsutula		0.23	0.14	0.97
Jaumea carnosa	−0.353***	0.77	0.73	0.07
Limonium californicum	0.177	0.71	0.32	4.38*
Salicornia virginica	−0.331**	0.97	0.82	1.97
Spergularia rubra		0.17	0.50	3.45
Triglochin concinna	0.523***	0.83	0.14	14.28***
Triglochin maritima		0.43	0.27	0.72
Species richness	0.591***			
Vegetation height	−0.405***			

Although *C. maritimus* is a facultatively parasitic species, its distribution may result from narrow habitat preferences rather than from host specificity (Chuang and Heckard 1971; Vanderwier and Newman 1984). Therefore, the identification of existing populations and viable sites for protection and restoration may depend on adequate knowledge of habitat suitability. Fink and Zedler (1990) found that suitable sites for reintroduction or recovery of *C. m.* subsp. *maritimus* populations were limited, but that site selection can benefit from an assessment of indicator species. The minimum size and most productive configuration of patches is also potentially important in recovery efforts because colonies of *C. m.* subsp. *maritimus* (Fink and Zedler 1990) and *C. m.* subsp. *palustris* (this study) can completely fail to appear in some years, although they may persist as seeds.

Plant species composition of upper salt marsh elevations where *C. m.* subsp. *palustris* occurs included several species (Table 1; nonenclature follows Hickman 1993) of varying abundance and distribution in northern California salt marshes (Macdonald 1988). Our first objective of study was to analyze patterns of co-occurrence of *C. maritimus* with other salt marsh plant species among populations on Tomales Bay, California. Secondly, to examine cover relation-

ships, we measured covariation of species cover values within the largest colony. Finally, we used data from the first three years of a monitoring program to assess patterns annual probability of *C. maritimus* colonies to appear among 35 colony sites on Tomales Bay, California.

STUDY AREA

Tomales Bay is a flooded, coastal fault-rift valley approximately 20 km long and 1–2 km wide, about 45 km north of San Francisco (Galloway 1977; Fig. 1). The largest salt marshes in Tomales Bay occur on the deltas of Lagunitas Creek at the southern end of the Bay and Walker Creek near the northern end of the Bay (Fig. 1). Numerous other smaller perennial and ephemeral streams enter the Bay along the east and west shores, each associated with a smaller, generally insular, delta salt marsh.

The *C. m.* subsp. *palustris* colony at Walker Creek Delta where we sampled plant species cover occupied approximately 2.5 of 40 ha. of salt marsh habitat and was undivided by tidal drainage channels. A low natural levee along the main creek channel north of the colony prevented the direct flow of freshwater from Walker Creek onto the salt marsh terrace, except during coincidental periods of extreme high tides and heavy runoff. Normal flushing of the marsh occurred through a separate tidal drainage on the south side of the colony.

METHODS

Co-occurrence. From 9 July to 20 August of 1991, 1992, and 1993, field surveys of *C. m.* subsp. *palustris* colonies were conducted on all potential habitat on Tomales Bay. For the purposes of this study, we defined a "colony" as a discrete patch of *C. m.* subsp. *palustris* separated by at least 10 m from the adjacent patch; we defined a population as a group of one or more colonies within a discrete salt marsh area, separated from other marshes by points of upland or more than 100 m of open water. The outer perimeters of all *C. m.* subsp. *palustris* colonies were marked annually and mapped, and the areal extent of each patch estimated as the product of the longest axis through the colony and its average perpendicular (colony width). Because sample units varied with the sizes of colonies and uncolonized salt marsh areas, species-area and other spatial scale effects prohibited direct comparisons of species richness or other community differences between colonized and uncolonized areas. However, to characterize habitat occupied by each colony, we visually ranked by relative cover the three most dominant species, visually estimated average density of *C. m.* subsp. *palustris* (low = 1–5 plants per m²; medium = 6–15; high = >15), and measured the shortest
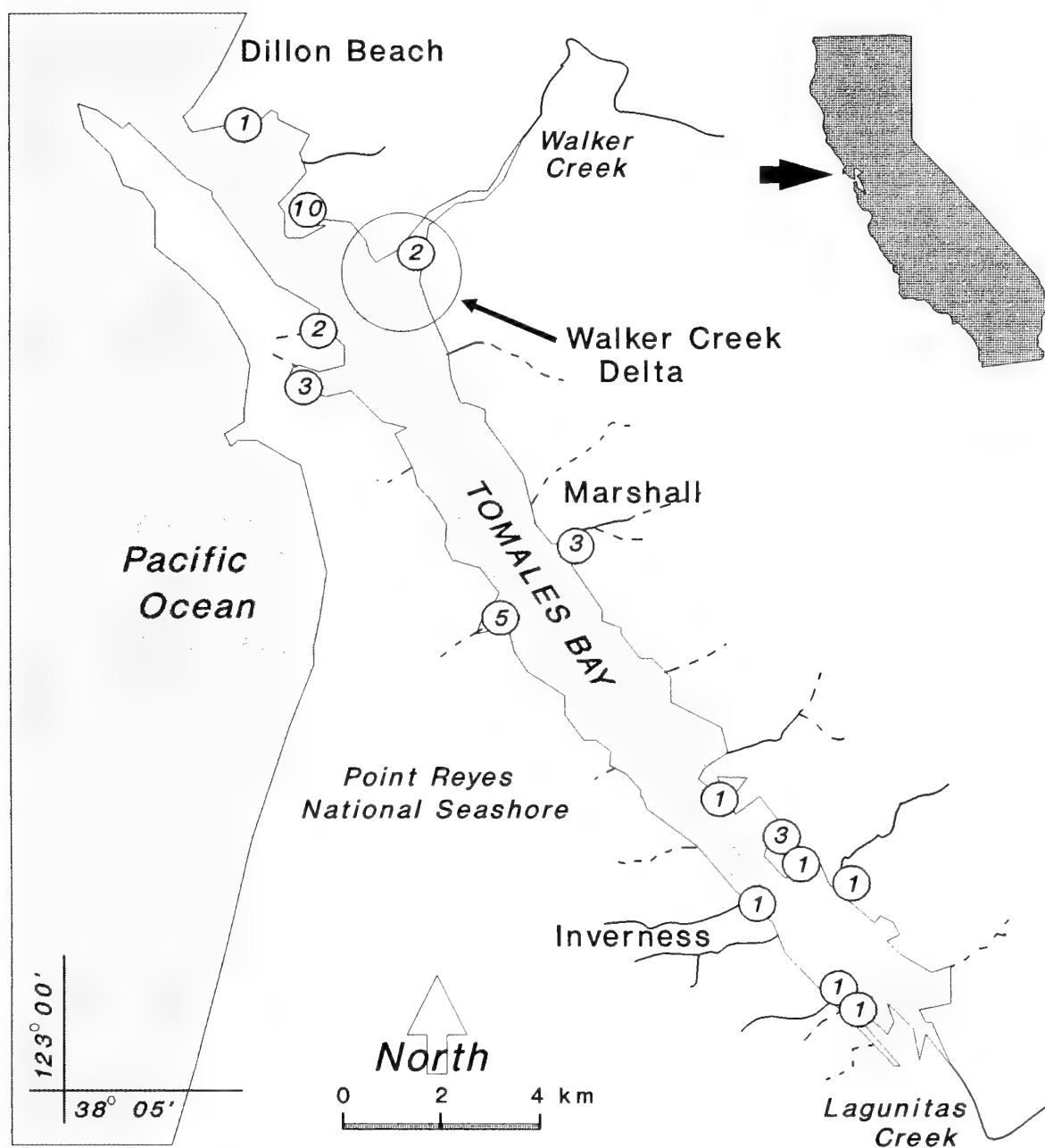
FIG. 1.   Distribution of *Cordylanthus maritimus* subsp. *palustris* populations (defined by discrete salt marsh areas) on Tomales Bay, California. The circled number at each population site indicates the number of colony sites observed from 1991 to 1993.

distance to upland vegetation and freshwater drainage. At each colony, and at each salt marsh where *C. m.* subsp. *palustris* was not found, we listed all other plant species present.

To assess habitat suitability, we used stepwise logistic regression (SLR), a technique that does not assume multivariate normality among predictor variables. The classification performance of the SLR model was tested against a chance model, assuming a probability of correct classification of each group by chance proportional to group size (Titus et al. 1984).

Cover. At Walker Creek Delta on 22 August 1989, we plotted three parallel transects through the largest area occupied by *C. m.*

subsp. *palustris* on Tomales Bay (Fig. 1). The transects were 420 m long, 10 m apart, and aligned parallel to the overall elevational gradient of the salt marsh. Peak seed-set occurred approximately 4 weeks earlier. One-square-meter sample quadrats were placed at 15-m intervals along each transect, following a random start from the edge of the *C. m.* subsp. *palustris* patch.

Percent cover by species was measured using a wire grid with 10-cm grid intervals attached to a square-meter sampling frame. The observer slid a straight section of wire vertically down each of the grid intersection points and recorded each species touched by the wire. The proportion of hits in each quadrat estimated percent cover by species. Next, the observer held the sampling frame level above each plot, approximating the plane of average vegetation height, then measured the height of the grid wires above the ground. Using stepwise multiple regression (SMR), we examined the relationship between (log-transformed) *C. m.* subsp. *palustris* cover values (dependent variable) and cover values of other plant species (independent variables); species richness and vegetation height were included as additonal candidate (independent) variables in the analysis.

Biogeographic relationships. We assessed the annual probability of *C. m.* subsp. *palustris* colonies to appear, based on three years of monitoring colony sites on Tomales Bay. Stepwise multiple regression was used to examine linear relationships between the number of years colonies were observed (maximum = 3) and eight (log-transformed) independent variables measuring biogeographic relationships: colony size (area), population size (sum of colony areas), distance to nearest colony, distance to nearest population, size of nearest colony, size of nearest population, colony density (estimated as described above), and number of colonies in the population.

RESULTS

We searched 35 salt marshes on Tomales Bay and identified 35 colonies among 14 populations of *C. m.* ssp. *palustris.* Half of the populations included only one colony and the most fragmented population included 10 colonies (Fig. 1). Colonies generally occurred at upper elevations of salt marshes, often in narrow bands near upper salt marsh edges. All *C. m.* subsp. *palustris* colonies on Tomales Bay (n = 35) were near ungrazed upland vegetation, usually mixed coastal prairie dominated by annual and perennial grasses (mean distance ± 1 SD = 18.0 ± 21.7 m, n = 35). Most colonies were also near sources of freshwater runoff (creeks or seeps; mean distance = 106.6 ± 170.3 m) and near plant species associated with freshwater or brackish habitat (mean distance = 36.4 ± 92.8 m).

The mean size of *C. m.* subsp. *palustris* colonies on Tomales Bay was 891 ± 4242 m²; however, most colonies were much smaller

TABLE 2. REGRESSION ANALYSES OF *CORDYLANTHUS MARITIMUS* SUBSP. HABITAT ON TOMALES BAY, CALIFORNIA. Tomales Bay-wide variation is analyzed with stepwise logistic regression (SLR) of presence/absence of *Cordylanthus maritimus* subsp. *palustris* (n = 57) on the presence/absence of co-occurring plant species in Tomales Bay salt marshes. Within-population variation is analyzed with stepwise multiple regression (SMR) of *C. m.* subsp. *palustris* cover (n = 87) on cover values of co-occurring plant species and species richness at Walker Creek Delta, Tomales Bay. * P < 0.05, ** P < 0.01, *** P < 0.001. [a] Probability cutpoint selected to balance correct classifications between groups.

Variable	*C. m.* subsp. *palustris* (presence on Tomales Bay [SLR])		*C. m.* subsp. *palustris* (cover at Walker Creek Delta [SMR])	
	Coefficient	SE	Coefficient	SE
(Constant)	−1.217		11.095	
Triglochin concinna	2.234	0.764**	0.059	0.016***
Limonium californicum	1.810	0.831*	−0.121	0.050*
Atriplex triangularis	−2.820	1.100*		
Species/m^2			1.263	0.244***
Log-likelihood = −22.03***			Model F = 22.92***	
Percent correctly classified = 86.0[a]			Adjusted R^2 = 0.43	
Cohen's kappa = 0.71***				

(median = 30 m^2, range = 0.1–25,200). The mean areal extent of populations was 1861 ± 6079 m^2 but most populations were much smaller (median 225 m^2, range 3–25,400). Average density estimates were less than 5 plants per m^2 in 58.8%, 65.2%, and 70.8% of colonies in 1991, 1992, and 1993, respectively. Weighting colony areas by mid-class density estimates, we obtained a rough estimate of median colony size of 225 plants (range = 3–75,000) and median population size of 1198 plants (range = 9–75,600). The three most dominant species (ranked by cover) among colonies most often included *Distichlis spicata* (97.1% of colonies), *Salicornia virginica* (60.0% of colonies) and *Triglochin concinna* (54.3% of colonies).

Univariate results from the Tomales Bay-wide survey suggested that the presence of *C. m.* subsp. *palustris* was significantly associated with the presence of *Triglochin concinna* and *Limonium californicum,* and the absence of *Atriplex triangularis* (Table 1). Pearson product-moment correlations of species cover values at Walker Creek Delta revealed that *C. m.* subsp. *palustris* cover was significantly greater in areas with greater *Triglochin concinna* cover, decreased cover of *Jaumea carnosa* and *Salicornia virginica,* greater species richness, and lower vegetation height (Table 1). Mean vegetation height at Walker Creek Delta was significantly lower in quadrats with *C. m.* subsp. *palustris* (x̄ = 12.5 ± 3.1 cm, n = 36), than in quadrats without *C. m.* subsp. *palustris* (x̄ = 16.5 ± 5.6 cm, n = 51; t = 3.88, P < 0.001, df = 85). Mean species richness at Walker

TABLE 3. OBSERVED AND PREDICTED (STEPWISE LOGISTIC REGRESSION) PROBABILITIES OF *CORDYLANTHUS MARITIMUS* SUBSP. *PALUSTRIS* OCCURRENCE ON TOMALES BAY, CALIFORNIA. Sample areas (n = 57) varied in presence (X) or absence (−) of *Triglochin concinna* (TRCO), *Limonium californicum* (LIMO), and *Atriplex triangularis* (ATRI).

TRCO	LIMO	ATRI	No. sample units	Observed proportion	Predicted by model ± SE
−	−	X	6	0.000	0.017 ± 0.021
−	X	X	4	0.000	0.103 ± 0.095
X	−	X	0	−	−
−	−	−	10	0.200	0.222 ± 0.112
X	X	X	3	0.667	0.496 ± 0.239
X	−	−	9	0.778	0.735 ± 0.128
−	X	−	5	0.800	0.653 ± 0.174
X	X	−	20	0.900	0.942 ± 0.041

Creek Delta was significantly greater in quadrats with *C. m.* subsp. *palustris* (x̄ = 6.7 ± 0.8, n = 36) than in quadrats without *C. m.* subsp. *palustris* (x̄ = 4.8 ± 1.4, n = 51; t = 7.33, P < 0.001, df = 85).

Stepwise logistic regression (SLR) predicted the presence of *C. m.* subsp. *palustris* among Tomales Bay salt marshes 71% better than chance alone (Table 2). *Cordylanthus maritimus* subsp. *palustris* was associated with the presence of *Triglochin concinna* and *Limonium californicum,* and with the absence of *Atriplex triangularis* (Table 2); the predicted probability of *C. m.* subsp. *palustris* occurring if all three of these conditions were met was 0.94 (Table 3).

The stepwise multiple regression (SMR) of plant species cover values at Walker Creek Delta associated greater *C. m.* subsp. *palustris* cover with greater *Triglochin concinna* cover, lower *Limonium californicum* cover, and greater species richness (Table 2). However, these three predictors accounted for only 43% of the variation in *C. m.* subsp. *palustris* cover among quadrats (Table 2); species richness alone accounted for 35% of the variation (r = 0.59, n = 87, P < 0.001).

Fifty-seven percent of *C. m.* subsp. *palustris* colonies on Tomales Bay appeared in all three years, 14% in two of three years, and 29% in one of three years. The preliminary SMR of number of years colonies appeared suggested that stability of colonies increased with colony size and density, and decreased with the number of colonies in the population (Table 4). The inverse relationship with number of colonies in a population reflected the stabilizing influence of larger colony size but not larger population size: colonies in smaller groups were generally larger (r = −0.42, P < 0.01, n = 35) but were not associated with larger populations (r = −0.04, P = 0.88, n = 14). Increased stability among larger colonies was also reflected in a significant inverse correlation between colony size and its coefficient

TABLE 4.   STEPWISE MULTIPLE REGRESSION OF NUMBER OF YEARS (MAXIMUM = 3) COLONIES OF *CORDYLANTHUS MARITIMUS* SUBSP. *PALUSTRIS* (n = 35) WERE PRESENT ON COLONY SIZE, NUMBER OF COLONIES IN THE POPULATION, AND DENSITY OF *C. M.* SUBSP. *PALUSTRIS* AT TOMALES BAY, CALIFORNIA. ** $P < 0.01$, *** $P < 0.001$.

Variable	Coefficient	SE
(Constant)	2.081	
Colony size (area)	0.162	0.048**
Number of colonies in the population	−0.579	0.191**
Colony density	1.128	0.375**
Model F = 11.28***		
Adjusted R^2 = 0.48		

of variation among years ($r = -0.59$, $n = 35$, $P < 0.0002$). The model predicted that an isolated colony with one to five individuals per m^2, occupying 281 m^2 of habitat, would have an average annual probability of appearing of 1.00 (SE = 0.064). However, the model is based on only three years of monitoring, and accounts for only about half of the variation in number of years colonies appeared (R^2 adjusted = 0.48). Variables associated with the sizes and distances of nearest other populations and colonies failed to enter the preliminary model. Bivariate correlations were not significant ($P > 0.05$) between number of years colonies appeared and both size of nearest population and distance to nearest colony; bivariate correlations with distance to nearest population ($r = -0.43$, $P < 0.01$, $n = 35$), size of nearest colony ($r = 0.43$, $P < 0.01$, $n = 35$), and size of population ($r = 0.35$, $P < 0.05$, $n = 35$) were significant, but did not significantly improve the SMR based on colony size and density.

DISCUSSION

Patterns of co-occurrence and covariation of cover values of *C. m.* subsp. *palustris* described in our study strongly suggest that *Triglochin concinna* is restricted to similar habitat, and should be considered as a potential principal host species. However, the distribution of *C. maritimus* probably depends more on habitat preferences than the distribution of a specific host (Chuang and Heckard 1971; Vanderwier and Newman 1984). During the hot, dry summers in southern California, the formation of haustorial connections probably permits *C. m.* ssp. *maritimus* to grow and flower, by providing access to water and/or nutrients late in the season when other annuals have completed their life cycles (Chuang and Heckard 1971; Vanderwier and Newman 1984). Experimental cultivation in pots indicated that *C. m.* spp. *maritimus* is more salt tolerant if grown with a host plant (Fink and Zedler 1989). However, *C. m.* subsp. *palustris* may depend less on the parasitic use of resources than *C. m.* subsp.

maritimus does because of more extended periods of seasonal rainfall and the regular occurrence of summer fog in northern California. Therefore, *C. m.* subsp. *palustris* may be less dependent on the distribution of host species on Tomales Bay than is *C. m.* subsp. *maritimus* in southern California salt marshes.

Limonium californicum was an important predictor of *C. m.* subsp. *palustris* among Tomales Bay marshes, and has been cited by others as an associate of *C. maritimus* (Chuang and Heckard 1971) and *C. m.* subsp. *maritimus* (Vanderwier and Newman 1984; Dunn 1987). At Walker Creek Delta, a positive (although non-significant) bivariate correlation between *L. californicum* and *C. m.* subsp. *palustris* cover contrasted with a negative SMR coefficient for *L. californicum*. The negative regression coefficient may have resulted from multicolinearity with other predictors, as suggested by positive bivariate correlations (n = 87) between *L. californicum* and both other variables in the model (*Triglochin concinna*: r = 0.44, P < 0.001; species richness: r = 0.51, P < 0.001). Thus, *L. californicum* typically occurred at low densities (percent cover = 14.0 ± 8.7, n = 87) that did not clearly reflect differences in *C. m.* subsp. *palustris* cover within m² quadrats, but was a valuable indicator of suitable habitat.

In contrast, *T. concinna* occurred in relatively dense patches (mean percent cover at Walker Creek Delta = 32.3 ± 27.6). At Tijuana Estuary, grasses were important associates of *C. m.* subsp. *maritimus,* possibly because their fine fibrous roots are easier for haustoria to find and penetrate (J. Zedler, personal communication). *Triglochin concinna* typically forms broad lawn-like patches (Howell 1970) and grows from spreading to ascending rhizomes (Thorne 1993), suggesting a greater host species potential with regard to root tissue availability.

The inverse relationship we found between *C. m.* subsp. *palustris* and *Atriplex triangularis* is probably an indication of habitat limitation. *Atriplex triangularis* is a characteristic species of upper marsh edges, occurring in both upper marsh and upland habitats throughout the salt marsh-grassland ecotone (Josselyn 1983; Macdonald 1988). On Tomales Bay, *A. triangularis* often occurred on small sandy delta marshes that retain relatively little tidal water, or on relatively dry sandy soils along the borders of low barrier dunes that form along the outer edges of delta marshes. Fink and Zedler (1988) cautioned against growing *C. m.* subsp. *maritimus* with *Atriplex watsonii* because of low numbers of flowers produced and reduced biomass during experimental cultivation in pots.

Vanderwier and Newman (1984) verified haustorial connections between *C. m.* ssp. *maritimus* and *Distichlis spicata* in the field, and found that *D. spicata* was the only species that was always associated with *C. m.* subsp. *maritimus* at Mugu Lagoon, California. In pot experiments of host associations of *C. m.* subsp. *maritimus,* Fink

and Zedler (1990) found the greatest above-ground biomass when plants were grown with *D. spicata*. *Distichlis spicata* occurred in nearly all of Tomales Bay-wide (94.7%) and Walker Creek Delta (96.6%) observations, regardless of *C. m.* subsp. *palustris* occurrence, and *C. m.* subsp. *palustris* cover at Walker Creek Delta was uncorrelated with *D. spicata*.

The SMR of plant species cover and richness accounted for less than half of the cover variation of *C. m.* subsp. *palustris* at Walker Creek Delta, but corroborated the value of *Triglochin concinna* suggested in the Tomales Bay-wide survey. However, the most important predictor of *C. m.* subsp. *palustris* cover was species richness rather than any particular species. Greater *C. m.* subsp. *palustris* cover in quadrats with greater numbers of species may reflect shared opportunities provided by greater light penetration in areas with lower overall vegetation height not dominated by *Salicornia virginica* (Table 1). Vegetation height was inversely related to species richness ($r = -0.54$, $P < 0.001$, $n = 87$) and directly related to *S. virginica* cover ($r = 0.61$, $P < 0.001$, $n = 87$). Clipping experiments by Fink and Zedler (1989) also suggested that habitat with greater light penetration should support greater seedling densities.

Although Zedler et al. (1992) reported peak growth of *C. m.* subsp. *maritimus* at 20% shade, our data do not suggest greater *C. m.* subsp. *palustris* cover in partially shaded areas. At Walker Creek Delta, vegetation height in quadrats containing *C. m.* subsp. *palustris* was low ($\bar{x} = 12.5 \pm 3.1$ cm), generally including some percentage of bare ground ($\bar{x} = 4.0 \pm 5.4$). We examined bivariate plots and found no evidence that greater *C. m.* subsp. *palustris* cover was related to partial overall cover, as indexed by vegetation height and bare ground. The value of partial shade may therefore be limited to relatively drier summer conditions found in southern California.

Zedler et al. (1992) reported the occasional failure of colonies to germinate, followed by reappearance after a year or two, and suggested the timing and amount of spring rainfull as possible controls. Therefore, a monitoring period much longer than our three-year study, encompassing a greater range of rainfall conditions is probably necessary to describe factors influencing the stability of colonies. The model we have presented provides a preliminary look at the relative importance of size, distance, and distribution among colonies, but should not be used to predict patch stability or minimum patch size.

Our results suggest that the annual probability of a colony appearing is influenced predominantly by colony size and density, and affected little, if at all, by the size or distance of nearby colonies or populations as sources for recolonization or outside recruitment. This is consistent with Dunn's (1987) suggestion that *C. maritimus* distributions are limited by a reduced probability of dispersal to new

locations within a marsh. The apparently low influence of nearby colonies suggests low dispersal probabilities that could limit resiliency to local disturbance. Colony size and density, and therefore the annual probability of a colony to appear, were likely influenced by other underlying factors or processes related to reproduction, growth, and/or survival, including soil salinity, light penetration, and availability of water or nutrients (possibly mediated by the availability of host plants).

Patterns of species co-occurrence and other habitat characteristics described in this paper should aid in predicting suitable habitat areas for *C. m.* subsp. *palustris.* These patterns also suggest that *Triglochin concinna,* and perhaps *Limonium californicum,* may be principal host species. Additional work is needed to understand the degree of isolation among colonies, i.e., to test our speculations that the stability of colonies is limited primarily by colony size and density rather than by the sizes or distances of neighboring colonies or populations, and that dispersal among populations may be insufficient to buffer the potential negative effects of local disturbance.

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NOTE

Stipa tenuissima (Gramineae) in Arizona — A Comedy of Errors—John R. Reeder, Herbarium, University of Arizona, Tucson, AZ 85721.

In 1947, W. B. McDougall (Bulletin 10 Grand Canyon Natural History Association, p. 20) reported *Stipa tenuissima* Trin. from Havasu Canyon [Coconino County], Arizona. The voucher is cited as: "Herbarium of the Museum of Northern Arizona, No. 4957." Neither the collector's name nor the date of the gathering is given. F. W. Gould (University of Arizona Biological Science Bulletin No. 7, p. 251, 252. 1951) also lists the species for Arizona. He states that it is known in the state by a single collection from Havasu Canyon, cites the McDougall publication, but adds that it "has not been examined by the writer." This last statement seems rather curious in view of the fact that Gould collected over much of Arizona, and one would think he could easily have stopped at the Museum in Flagstaff on one of his trips. Moreover, the specimen could probably have been borrowed. There seems to have been no serious attempt to verify the report. Although Swallen, who authored the treatment for the Gramineae in Kearney & Peebles Arizona Flora (1951), does not include *S. tenuissima,* there is no mention of the former reports of the species in the State.

In 1955 *Stipa tenuissima* is again listed as occurring in Arizona in a work by C. F. Deaver & H. S. Haskell (Plateau 28:15). Their listing is "bare bones." They merely give the name, preceded by two symbols, * and x, which they inform us indicate that the name was in McDougall's 1947 list, and that the record is based on a single collection. To my knowledge, this third published listing of *Stipa tenuissima* in Arizona is the final one.

In 1987, B. G. Phillips, A. M. Phillips, & M. A. Schmidt Bernzott published an updated checklist for Grand Canyon National Park (Monograph 7, Grand Canyon Natural History Association). In this publication, there is no mention of *Stipa tenuissima.* In fact, nowhere in the literature have I found any explanation of why the species has not been included in literature on Arizona grasses since 1955.

In an attempt to clarify this problem, I requested from the Museum of Northern Arizona (MNA) a loan of the sheet on which the various reports had been based. Although McDougall did not identify the collector, he stated that the specimen was [Museum accession] no. 4957. The Curator at MNA, Scott Cutler, kindly searched out the specimen and sent it for our examination. The herbarium sheet proved to be most interesting. The specimen was collected by A. F. Whiting, his number *1047.* The label data are: Havasupai Canyon, Agency. May 24, 1941. Elev. 3200 ft. The binomial "Stipa tenuissima Trin.", along with a notation "apparently *State Record*" is written on the sheet in longhand. This is in Lyman Benson's script, and after "Determination by" at the bottom of the label, Benson has signed his name and added "1941". Above the label, however, is an annotation as *Stipa arida* [M. E.] Jones made by T. H. Kearney in 1945! Kearney's determination is correct.

It is curious, indeed, that McDougall would have reported this collection as *Stipa tenuissima* two years after Kearney had annotated the sheet correctly as *S. arida,* a quite different species which is not uncommon in southwestern U.S. In fact, ARIZ has several collections of *S. arida* from both Coconino and Mohave counties in our State. As indicated above, this error was perpetuated twice more: by Gould (1951), and by Deaver & Haskell (1955). Again, I have seen nothing in the literature to indicate that these reports were based on a misidentification which was corrected two years before the first publication of this "record."

On page 19 of the Phillips et al. publication (1987) one finds *Stipa arida* listed

from Havasu Canyon, but there is no indication that this is the plant which had been reported over a period of ten years, in three different publications, under the name *Stipa tenuissima.*

Below is a summary of the errors involved with *Stipa tenuissima* in Arizona.

1.   The Whiting specimen was originally incorrectly identified by Lyman Benson.
2.   McDougall (1947) reported the misidentification as a new record for Arizona, even though the sheet had been correctly annotated as *S. arida* by T. H. Kearney two years earlier.
3.   Gould (1951), although preparing a comprehensive grass flora of the State, listed *Stipa tenuissima,* but apparently made no attempt to see the specimen on which the report of the species was based.
4.   Swallen (1951), must have realized (or suspected) that the report of *Stipa tenuissima* was in error since he did not include it, but he offered no explanation.
5.   Deaver & Haskell (1955) again listed *Stipa tenuissima* in their Plants of Havasu Canyon. This was ten years after the Whiting specimen (the sole basis of the former reports) had been correctly annotated as *Stipa arida.*
6.   Phillips et al., in their 1987 checklist of the plants of Grand Canyon National Park, list *Stipa arida* from Havasu Canyon. Nowhere in the publication, however, is there any reference to the Whiting specimen (from Havasu Canyon) which had been erroneously determined as *Stipa tenuissima,* and had served as the only basis for inclusion of the latter species as part of the Arizona grass flora.

Although *Stipa tenuissima* is known from New Mexico and Texas, I know of no authentic record of this species from Arizona. Except for the Whiting specimen cited above, the only other collection I have encountered from Arizona labeled *S. tenuissima* is a sheet at ARIZ, *L. N. Goodding 233-58,* from Cochise County, 26 July 1958. The specimen is actually *Stipa eminens* Cav. and has been so annotated by the author of this note.

It is curious, indeed, that McDougall would have reported this collection as *Stipa tenuissima* two years after Kearney had annotated the sheet correctly as *S. arida.* As indicated above, this error was perpetuated twice more: by Gould (1951), and by Deaver & Haskell (1955). Again, I have seen nothing in the literature to indicate that these reports were based on a misidentification which was corrected two years before the first publication of this "record."

NOTEWORTHY COLLECTIONS

ARIZONA

FUIRENA SIMPLEX Vahl var. SIMPLEX (CYPERACEAE).—Gila Co., Tonto National Forest, Sierra Ancha Wilderness Area. Collected on 22 Sep 1991 along the wilderness boundary, at a spring along Oak Creek, just W of Coon Creek Butte, T5N, R14E, S22, SW1/4 of NW1/4, elev. ca. 1450 m (4800 feet), *Imdorf & Dow 293* (ASU).

Previous knowledge. Range of the species extends from southern Kansas and Illinois southward into Texas and New Mexico, and through Mexico, including Baja California, into Nicaragua; in the Caribbean in Cuba, Jamaica, and Puerto Rico (R. Kral, A synopsis of *Fuirena* (CYPERACEAE) for the Americas north of South America, Sida 7(4):309–354, 1978).

Significance. This collection represents the first report of both the genus and species in Arizona. The Arizona plants are disjunct from the nearest known populations: Baja California (near Ensenada, ca. 550 km to WSW); Eddy Co., New Mexico, and Culberson Co., Texas (both ca. 600 km to ESE); and Sonora (near Bahia San Carlos, ca. 675 km to S).

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PSILOTUM NUDUM (L.) Beauv. (PSILOTACEAE).—Pima Co., Rincon Mountains, Chimenea Canyon, Saguaro National Monument East, ca. 1.25 mi N of Madrona Ranger Station, vicinity of 32°10'04"N,110°36'52"W,ca.4120'(1260 m). Eight individuals were found growing in a boulder seam with *Pellaea truncata,* completely shaded by large leaning boulders in a steep canyon bottom with *Vitis arizonica* and *Juglans major;* on the slopes nearby were *Agave schottii, Carnegiea gigantea, Cercidium microphyllum, Fouquieria splendens. Shelley McMahon 146, Mark Fishbein, Amy Johnson* (8 May 1994, ARIZ, MO).

Significance. Second record for Arizona. Only other record for Arizona, consisting of a single individual (*Kaiser s.n.* (4 Feb 1968, ARIZ)) was found ca. 105 km southwest of the Rincon location in Sycamore Canyon, Pajarito Mountains (Phillips, Amer. Fern J. 60:30–32, 1970). The next closest populations are disjunct in northwestern Mexico, the nearest by more than 450 km: near Guaymas, Sonora in Nacapules Canyon (Boutin, Amer. Fern J. 61:142–143,1971), in the Sierra Saguaribo of southeastern Sonora (Gentry, Rio Mayo Plants, Carnegie Inst. of Wash. Pub. #527, 1942), and in the Barranca del Cobre of southwestern Chihuahua (Knobloch and Correll, Ferns and Fern Allies of Chihuahua, Texas Research Foundation, 1962). Elsewhere, *P. nudum* is found in moist woods in the southeast United States and in Asian, African and American tropics and subtropics, making the Sonoran desert populations remarkable.

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OREGON

ACORUS CALAMUS L. (ARACEAE).—Marion Co., Salem, gravel bar in Mill Creek, 7 July 1922, *J. C. Nelson 4387* (OSC, WS). The specimen at WS is dated 7 June 1922.

Previous knowledge. Opinions differ whether this species is irregularly circumboreal, or native only to Eurasia and adventive elsewhere. Throughout much of North America east of the Rocky Mountains. In the Pacific Northwest, reported from Montana, Idaho and eastern Washington (Hitchcock et al., Vascular Plants of the Pacific Northwest, Vol 1, 1969), British Columbia (Brayshaw, C. T., Pondweeds and bur-reeds, and their relatives, of British Columbia, Occ. Pap. B. C. Provincial Museum 26, 1985) and northern California (McClintock, E. in J. C. Hickman (ed.), The Jepson Manual, Higher Plants of California, 1993).

Significance. Never reported from Oregon by either Peck (A Manual of the Higher Plants of Oregon, 2nd ed., 1961) or Hitchcock et al. (1969). Despite this oversight, it was mapped as occurring in Oregon by Muenscher (Aquatic Plants of the United States, 1944). The species apparently has not been collected in Oregon since it was first found in 1922.

CABOMBA CAROLINIANA A. Gray (CABOMBACEAE)—Clatsop Co., becoming abundant in several sloughs near Astoria, 13 December 1962, *J. H. Wood s.n.* (OSC). Seen recently but not collected in Cullaby Lake, West Lake and Cullaby Creek, all in coastal Clatsop Co., where it is very abundant.

Previous knowledge. Native throughout much of eastern North America, as far west as Illinois, Oklahoma and Texas. Cultivated widely for the aquarium trade, this species has escaped and is becoming naturalized in the Pacific Northwest. Populations seen in Oregon and Washington are robust, reproducing vegetatively, and hardly resemble "waifs"noted by Stone (in Hickman (ed.), 1993).

Significance. The 1962 collection at OSC was unknown or overlooked by Hitchcock et al. New to Oregon and Pacific Northwest.

MIMULUS RINGENS L. (SCROPHULARIACEAE)—Columbia Co., Columbia River, along slough between railroad and river channel just N of Rinearson Slough, 4 mi NW of Rainier, T7N, R3W, sec. 2, 1 July 1992, *J. A. Christy 8110* (OSC). Seen or collected in four other localities along the Columbia River between Lord Island, Columbia Co., and Sand Island, Multnomah Co.

Previous knowledge. Native throughout much of eastern North America east of the Rocky Mountains. In the Pacific Northwest, reported from Washington (Maxwell, C. L., Vascular flora of the Willapa Hills and lower Columbia River area of southwestern Washington, Douglasia Occ. Pap. 4:27–76, Washington Native Plant Soc., 1991) and Idaho (Davis, R. J., Flora of Idaho, 1952; Cronquist et al., Intermountain Flora, Vol. 4, 1984).

Significance. New to Oregon. The species is becoming widespread on mud and sand in the freshwater intertidal zone along the Columbia River below Bonneville Dam, where populations number from one to hundreds of individuals. On the Washington side of the river, populations were seen as far upriver as Cottonwood Island, just above Longview, in Cowlitz County.

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WASHINGTON

ACORUS CALAMUS L. (ARACEAE).—Clark Co., 0.8 km SW of La Center, population ca. 50 feet in diameter, open *Salix lasiandra* bottomland on East Fork of Lewis River, T4N, R1E, sec. 4, 21 October 1992, *J. A. Christy 8263* (OSC).

Previous knowledge. Distribution is given above in report for Oregon. In Washington, reported previously from Spokane Co. by Hitchcock et al. (1969).

Significance. First report from western Washington.

CABOMBA CAROLINIANA A. Gray (CABOMBACEAE)—Cowlitz Co., Columbia River, submersed in Coal Creek Slough, 9.5 km NW of Longview, T8N, R3W, sec. 15, 19 October 1992, *J. A. Christy 8261* (OSC). Seen recently but not collected in nearby Solo Slough and Willow Grove Slough, Cowlitz Co.

Previous knowledge. Distribution is given above in report for Oregon.

Significance. New to Washington.

MURDANNIA KEISAK (Hassk.) Hand.-Mazz. (=*ANEILEMA KEISAK* Hassk.) (COMMELINACEAE).—Wahkiakum Co., Columbia River, Grays Bay, intertidal freshwater marsh just W of Pigeon Bluff, on mud with *Alisma plantago-aquatica* and *Carex lyngbyei*, 4 mi SSW of Rosburg, T9N, R8W, sec.9, 28 July 1992, *J. A. Christy 8163* (OSC).

Previous knowledge. Native to eastern Asia. Reported from southeastern United States as far west as Arkansas (Gleason, H. A, and A. Cronquist, Manual of Vascular Plants of Northeastern United States and Adjacent Canada, 2nd ed., 1991). In the Pacific Northwest, reported from Oregon (Thomas, D. W., The vascular flora of the Columbia River estuary, Wasmann J. Biol. 42:92–106, 1984).

Significance. New to Washington.

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LASTHENIA MINOR (DC.) Ornduff (ASTERACEAE).—Skagit Co., Pass Island, Deception Pass, open rocky area ca 30 m east of the parking area near summit, 5 June 1991, *E. Kozloff s.n.* (UC; WTU).

Previous knowledge. Otherwise known from scattered localities in California along the coast from Mendocino County to San Luis Obispo County and the Central Valley and adjacent valleys from Amador and Solano counties to Kern and San Luis Obispo counties (Ornduff: Univ. Calif. Pub. Bot. 40, 1966; The Jepson Manual, 1993).

Comment. The Kozloff collection consists of low, depauperate plants with 1–3 small capitula per plant; the population was first observed by him in 1990. We first assumed the specimens were referable to *L. maritima* (A. Gray) M. Vasey because of their insular habitat and the occurrence of that species to the west on islands off the northwestern coast of the Olympic Peninsula and off the west coast of Vancouver Island (Vasey: Madroño 32:131–142, 1985). Achenes collected by Kozloff in June, 1992, were sown by Ornduff in a cool greenhouse in early 1993. The resultant plants were randomly cross-pollinated and capitula with nearly mature achenes were removed from six individuals and sent to Vasey for scoring, using the 20 characters he employed to discriminate between *L. minor* and *L. maritima*. In 11 of these characters (including ligule length, number of awns, number of pappus scale divisions, ratio of ligule to phyllary length, and number of achene hairs) the plants match *L. minor*; these are generally the "best" morphological characters for distinguishing between the two species as suggested by the t-values in Table 3 of Vasey's 1985 paper. In two characters (scale length, scale/awn length) the plants resemble *L. maritima*; and in seven characters (including phyllary length, achene length, awn length) the measurements are non-definitive. The short scale length and relatively glabrous achenes of the Washington plants are matched elsewhere only by plants of *L. minor* from the

southern portion of its California range. *Lasthenia minor* is strongly self-incompatible; *L. maritima* is strongly self-compatible, with high levels of autogamy in plants grown in insect-free greenhouses (Ornduff 1966). Single capitula of six cultivated specimens of the Washington plants were self-pollinated in 1993 and the mean achene-set of such plants was 5.1 percent. Single capitula of three individuals in this progeny were artificially cross-pollinated with other plants; their mean achene-set was 54.8 percent. While the latter figure may seem low, mean achene-set of 13 plants of *L. minor* in a natural population at Kehoe Beach, Marin Co., California, examined in May, 1993, was only 69.0 percent, a figure not remarkably higher than that obtained from the artificial cross-pollinations of the cultivated material from Washington. Thus we conclude that the Washington plants are self-incompatible. *Lasthenia maritima* nearly always occurs on soils derived from seabird guano, whereas *L. minor* very rarely occurs on such soils (Ornduff 1966; Vasey 1985). The Washington population does not grow on guano-enriched soil. Thus, on the basis of morphological characters, breeding system, and edaphic occurrence, we assign the Washington plants to *L. minor*. This disjunct population of *L. minor* occurs over 1000 km north of the nearest natural population of the species near Cleone, Mendocino County, California. It is possible that the Washington population originated from an accidental human introduction to the site, since the area is heavily visited by tourists. However, the distinctive combination of morphological characters of the Washington population of *L. minor* is unknown in California populations and leads us to believe that the Washington population may represent a natural disjunction of sufficient antiquity that morphological divergence has occurred.

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REVIEWS

Ecology and Evolution of Plant Reproduction: New Approaches. Edited by ROBERT WYATT. 1992. Chapman and Hall, New York. 397 p. Hardcover, $73.95. ISBN 0-412-030-217.

Plant reproductive biology has a long history, but until only a short while ago it was dominated by natural history approaches. In the early 1970's, studies on pollen movement joined ecological studies of seed production and natural history studies of pollination. But the study of plant reproduction has completely changed in character during the last 10–15 years. There seems to be an integration among population genetic, ecological and evolutioary approaches more than in other areas of biology. In the preface, Robert Wyatt describes these changes as an "intellectual revolution" and this seems a fair description, if this book represents a sampling of research in the field.

Fourteen chapters introduce us to the new directions this field is taking. Wyatt mentions in the preface that "the purpose of this book is to make some of the exciting new discoveries in this field accessible to a wide audience." This objective has been well achieved. All of the chapters represent excellent summaries of different research areas. But in addition to the usual review of new areas, most chapters also present original research. Such a combination makes this collection of articles much more interesting and unusual in contrast to the typical edited book on a research area.

Several chapters focus on pollen flow, dispersal and performance from a variety of approaches. Among these the chapter by James D. Thomson and Barbara A. Thomson on pollen presentation and viability schedules in animal-pollinated plants was particularly interesting. They started off with a good review of what's known about pollen presentation scheduling and pollen viability patterns. They followed this with a presentation of a computer model based on their field work studying *Erythronium*. The model was used to explore different patterns of pollen viability and different types of pollinator behavior. For example, they described three pollinator types, Good, Bad, and Ugly pollinators, which combined different degrees of pollen removal and redeposition. The model showed how these pollinator types varied in their effectiveness depending on the context of circumstances: timing, length of pollen viability, timing of ovule presentation, and other features. This was an excellent combination of using detailed field collected data with computer models.

Another well-written chapter was one by Maureen L Stanton, Tia-Lynn Ashman, Laura F. Galloway, and Helen J. Young on estimating male fitness of plants in natural populations. Like the Thomsons' chapter, they started out with an excellent review of issues and literature. This was followed by some additional experimental field work related to specific issues they wanted developed. A computer model was also developed to pursue some additional thoughts. I liked this chapter because they did go the extra step to bring the reader completely into the field they are investigating, and then approached it from both experimental and modeling directions in a way I found quite interesting.

Two chapters by David Lloyd and Kent Holsinger delved directly into evolutionary theory. At first both chapters seemed a little intimidating because of the mathematical approaches, but surprisingly I found both easy to follow. Similarly, both come to conclusions quite different to what I was expecting. Lloyd investigates evolutionarily stable strategies of reproduction in plants and starts off with the expression "we are in the midst of a revolution in studies of plant reproduction." He describes how the rise of evolutionary ecology has brought an emphasis on evolutionarily stable strategies (ESS's) for the deployment of pollination and dispersal mechanisms. Lloyd then

argues that selection hypotheses put forward to explain adaptive strategies must rest on a sound theoretical basis. He goes on to examine the theoretical justification for aspects of kin selection and male-female conflict. He concludes that there is no single universal answer as to whether calculations of collective or inclusive fitness give more useful descriptions of the selection of social acts in plant reproduction. Lloyd cautions that each phenomenon must be carefully examined, that kin selection formulations are not always accurate and that they have sometimes been invoked inappropriately in the past. "We cannot simply assume that kin selection is the preferred mode for describing the action of natural selection whenever we are dealing with social acts among relatives. In the future, kin selection formulations should be employed more advisedly, only when they give an accurate description of events." Holsinger explores the evolution of plant mating systems in the context of selfing in plant reproduction. He starts by making distinctions concerning inbreeding depression at the population level and at the sibling level. He then develops an alternative model, the mass-action effect model to investigate the origin and maintenance of selfing in populations. Using this model, Holsinger is able to show how plant mating systems may depend on the density of individuals and the frequency of mating types rather than on some intrinsic selective advantage. He describes his model as a hybrid between population genetic traditions that associate selfing with reproductive advantage with ecological studies that show environmental conditions may play an important role in determining when selfing evolves.

Among the other chapters, my favorite was one by Pamela K. Diggle on development and the evolution of plant reproductive characters. My interest in this chapter may result simply from how much I learned, but I think also because it is an introduction to an aspect of evolution that we all know is "important," but is not well-integrated into our thinking and experimental approaches, showing up only now and then. This chapter does an excellent job of bringing in developmental models like heterochrony, progenesis and neotony and clearly illustrating how in some circumstances they can influence floral morphology and reproductive syndromes.

All in all this is an excellent book that really does accomplish the objective of making the current research in reproductive biology accessible to a larger audience, and it does it in a generally exciting and interesting way. The book is well-edited and I found only one typo. Most chapters are well-illustrated although even more would have been helpful. Because it is a multi-author book, some chapters suffer from being combined with really well-written and clear chapters. I noticed that if I read the same chapter on different occasions, my opinion of it could increase considerably just due to the lack of contrast with the better-written chapters.

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Flora of North America, Volume 2, Pteridophytes and Gymnosperms. Edited by Nancy R. Morin. Oxford University Press, New York. xvi + 475 p. Hardcover, $75. ISBN 0-19-508242-7.

Much has already been written concerning the landmark publication of the first two volumes of Flora North America (FNA). The monumental efforts of Dr. Nancy Morin, the editorial committee, and the contributing authors have deservedly met with near universal praise. Rather than repeat the accolades of other reviewers, I will discuss the taxonomic treatments of Volume 2 from my perspective as a systematist interested in plant evolutionary relationships and conservation biology.

One of the major goals of FNA is the synthesis and incorporation of the systematic research relevant to each taxon. Through the combined efforts of the authors and editors, the coverage of the taxonomic and floristic literature is superb. More remarkably, the majority of the accounts of the ferns have successfully assimilated results from cytogenetics and enzyme electrophoresis. The groundbreaking work on hybridization in *Asplenium* initiated by Herb and Florence Wagner in the 1950's served as the model for further biosystematic studies of ferns, much of it conducted in the last 20 years. The power of these studies, and the influence of the Wagners, is likely responsible for the inclusion of reticulograms in many of the fern treatments. These figures do an excellent job of summarizing our remarkably good knowledge of reticulate evolution in the ferns. Hypotheses of evolutionary relationships are best summarized in diagrams, and it is hoped that FNA will continue to incorporate reticulograms *and* cladograms (none are found in Volume 2) in future volumes.

It is encouraging to see that many of the fern treatments have been written by the same systematists who conducted the complementary experimental studies. This has resulted in treatments that include important biological insights into the distribution and evolutionary history of the taxa. In addition, the extensive field experience of these pteridologists results in comments like "this species is most often confused with . . ." which will greatly assist the users of FNA. However the field botanist may not appreciate all of the experimental results incorporated into Volume 2. For example, only isozyme analysis can discriminate the morphologically identical gametophytes of *Trichomanes intricatum* (its sporophytes are unknown) from those of other *Trichomanes* species! In practice these gametophytes would be more readily confused with algae or moss protonemata, the introduction to the genus gives helpful distinguishing features.

While the brief discussions following the taxonomic descriptions are full of valuable information not easily found elsewhere, I found myself frustrated by the general lack of discussion for the classifications used in the various treatments. The introduction to Volume 2 states that "with few exceptions taxa are presented in taxonomic sequence. If an author is unable to produce a classification, the taxa are arranged alphabetically, and the reasons are given in the discussion." In my opinion, it is the "taxonomic sequence" that requires explicit justification. On the other hand an alphabetical arrangement conveys to me the generally honest assessment that we "just don't know " enough about the relationships. And assuming an author does have a well-founded hypothesis of phylogenetic relationships for a genus—how is this to be converted to a linear sequence of taxa? Authors have interpreted the requirement to produce a "taxonomic sequence" in various ways. Many list the species of a genus in the order that they appear in the key, others list them alphabetically throughout or within (often undefined) subgroups, and a few appear to have arranged them according to an unspecified taxonomic scheme. The same inconsistency of approach exists for the higher taxonomic groups. At the generic level and above our understanding of phylogenetic relationships is currently being revolutionized by the study of nucleic acid sequences. Thus it is likely that much of the taxonomic sequence in Volume 2 will appear very dated by the time FNA is complete, whereas an alphabetical arrangement would remain valid for a significantly longer period of time.

A total of 66 North American pteridophytes have been either newly described or placed in new combinations since 1984. (Incidentally, this information was retrieved by accessing the FNA database at the Missouri Botanic Garden and searching for year of publication; this demonstrates the utility of an extremely important adjunct to FNA.) Much of this taxonomic work is supported by experimental studies, leading to a treatment that clearly distills the "state of the art" in pteridophyte systematics.

In contrast to the fervent taxonomic activity in ferns, only two new taxa have been published for the FNA gymnosperms in the last decade. While numerous studies relevant to our systematic understanding of the gymnosperms have been carried out during this period, and some of these are cited in FNA, the implications of these studies are generally not incorporated into the taxonomic accounts. Examples include

the genetic studies of the *Pinus ponderosa* and *Pinus contorta* species complexes. Perhaps this results from the fact that the studies are done by forest geneticists, and not the systematists contributing to FNA. This is unfortunate, for it means that FNA's goal of synthesizing the "wide-ranging botanical data" remains unfinished in the case of the gymnosperms.

In Volume 2, 45 taxa are flagged "of conservation concern" (thanks again to the FNA database for allowing easy compilation of this figure). Remarkably, over 50% of these taxa are confined to three genera, *Selaginella* (9), *Isoetes* (7), and *Botrychium* (10). Unfortunately, many of the FNA accounts contain little or no information as to why a particular taxon has been deemed of conservation concern. Why for example is *Selaginella oregana* of concern while *Botrychium ascendens* is not? The former is not considered on any state, federal, or Natural Heritage Program list, while the latter is a candidate for federal listing under the Endangered Species Act and is on state lists in California, Oregon, and Washington. For the term "of conservation concern" to be useful, a discussion of its application in a particular situation should always be given.

Persons interested in plant conservation will also look to the distribution maps provided for each and every taxon. All distributions are presented on a standard base map of North America. This is useful for visualizing diverse biogeographic patterns such as widespread taxa, local endemism, and disjunct distributions. However, from a conservation perspective, this "one size fits all" approach is less helpful. For example, the distribution of *Pinus torreyana* ssp. *insularis* can only be obtained from the text since the "spot" is larger than "specks" that represent Santa Rosa and neighboring islands. I realize that a continental flora cannot provide detailed information on the local distribution of each species in the same way that a national weather forecast won't tell me the probability or rain tomorrow in Corvallis. Since this is the case, references to where to find more detailed distribution maps would be a helpful addition. Also I could not find an explanation for the dark vs. light shading on the maps—apparently the former is used for scattered occurrences over the indicated range (cf. *Sequoiadendron giganteum* and *Cupressus* spp.) as opposed to a more continuous distribution. Finally, I must point out that *Botrychium pumicola*, the only Oregon endemic in Volume 2, is not restricted to Greenland as its unintentionally misplaced map would suggest. Fortunately its distribution is described in the text in more detail than most.

I must admit that I feel a bit ungrateful concentrating on the few shortcomings of Volume 2 and offering unsolicited advice to the FNA editorial committee. For this milestone volume is without a doubt of tremendous benefit to the study of North American botany and its positive contributions far outweigh the minor imperfections. No botanical library will be complete without the Flora of North America, and I eagerly await the appearance of future volumes.

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Editor's Report for Volume 41

This annual report serves to tell members of the society the status of Madroño from manuscripts submitted to papers published. Since I assumed the duties of Editor of Madroño late in 1993 sixty-seven manuscripts have been submitted, including articles, notes, noteworthy collections, reviews, and obituaries. Forty-one have been published, and forty-seven others are either in some stage of review or in the queue to go to press. During this period surprisingly few articles were rejected by Madroño. This is due to the high quality of reviews as well as the dedication with which authors respond to the comments and suggestions of reviewers. I deeply appreciate authors' attention to details that editors usually require.

A noteworthy milepost was passed this year by Madroño—the publication of the first (I believe) paper dealing with molecular (DNA) systematics. I find this noteworthy because it underscores the interest of the Madroño readership in continuing to celebrate new approaches to science while valuing approaches that have served, and continue to serve, the botanical community.

Next year will see another milepost for Madroño—an issue devoted to the publication of last June's Symposium of The Future of California Floristics, held at UC Berkeley.

Throughout this year I have enjoyed reading the diverse array of manuscripts that were submitted to Madroño. I wish to encourage authors to continue sending manuscripts to a journal that values the diversity of research that marks the California Botanical Society. I, along with 1994–1995 president Wayne Ferren, wish also to invite papers of a point-of-view nature, if there are authors that feel that Madroño is an appropriate place to share their thoughts.

As I read last year's (vol. 40) Editor's report I see outgoing editor Jon Keeley remarking on my "enthusiasm for taking on the editorship for the next three years." At this point my enthusiasm continues, but so too does my gratitude to the many who have made this year's editorship smooth. First, Jon Keeley made the transition from his editorship to mine painless, interesting, and fun. He continues to be a valuable consult on editorial matters. Jon also continues to serve (he volunteered!) as the editor for book reviews. John Strother, who first got me interested in the editorial process years ago, is my primary resource for solving editorial problems (they're only problems to me—rarely are they to John). I am indebted to Steve Timbrook, my old compadre, for providing the index and table of contents for volume 41. I owe a deep gratitude to my "secretary" and graduate student, Isabelle de Geofroy, for keeping things in order. And another note of appreciation goes to Jim Kelley, Dean of the College of Science and Engineering at SFSU, for being enthusiastically supportive of my editorship by committing funds to hire Isabelle. I hope that future editors will enjoy the level of support that I have from San Francisco State University. Annielaurie Seifert at Allen Press has been especially helpful and calming with matters of the press. Outgoing president Peggy Fiedler and the CBS executive council have been helpful and responsive to my editorial needs during this first year. Finally I thank the reviewers who have given their time and effort to ensure that Madroño remains a quality journal. Their names appear on a separate page of this issue.—Robert Patterson.

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INDEX TO VOLUME 41

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members of the California Botanical Society, and membership is prerequisite for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or "erasable" paper. Avoid footnotes except to indicate address changes. Abbreviations should be used sparingly and only standard abbreviations will be accepted. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to $^2/_3$ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include a scale and latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used by Sivinski, Robert C., in Madroño 41(4), 1994. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th ed. Names of authors of scientific names should be abbreviated according to Brummitt and Powell, *Authors of Plant Names* (1992) and, if not included in this index, spelled out in full. Titles of all periodicals, serials, and books should be given in full. Books should include the place and date of publication, publisher, and edition, if other than the first.
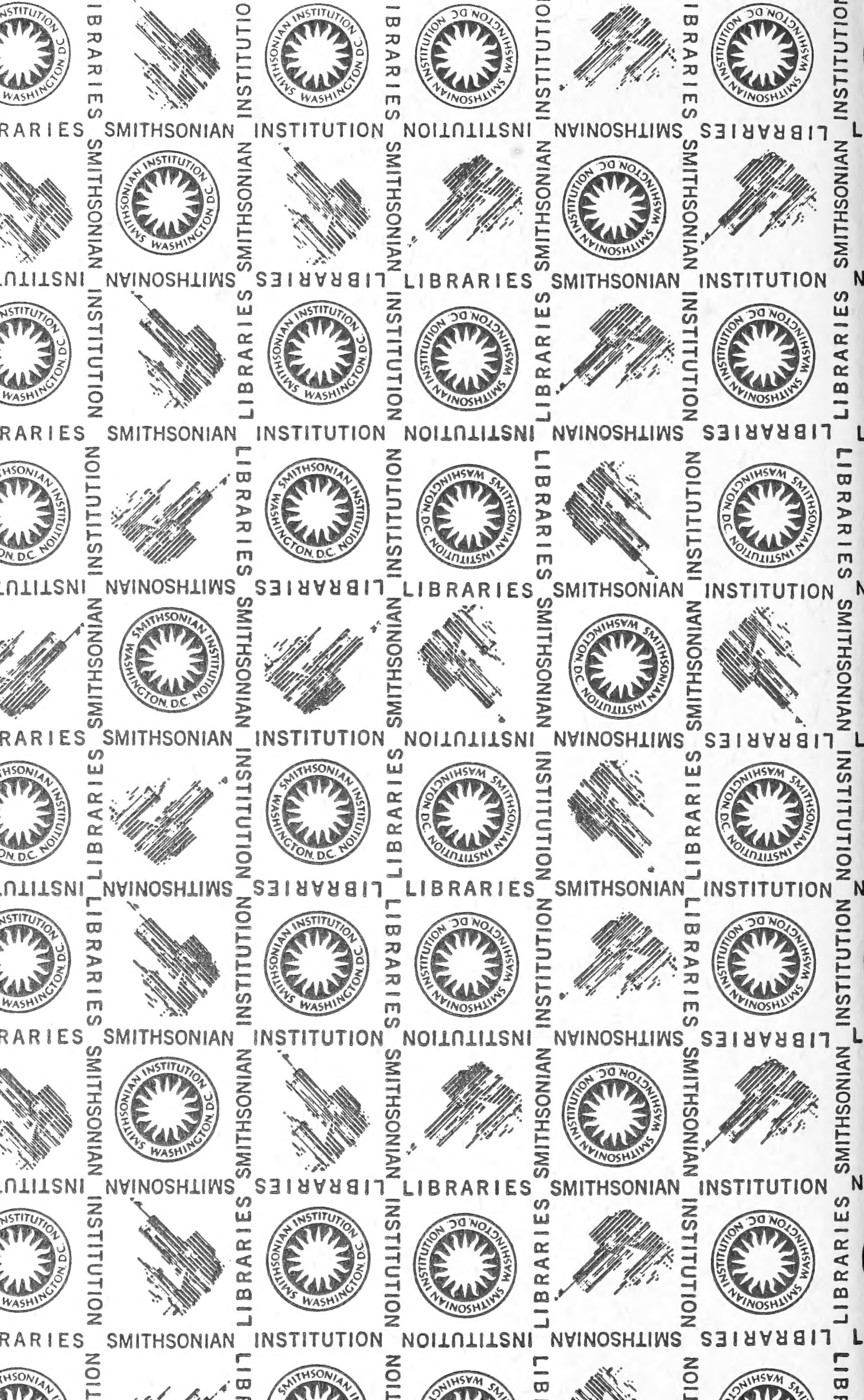
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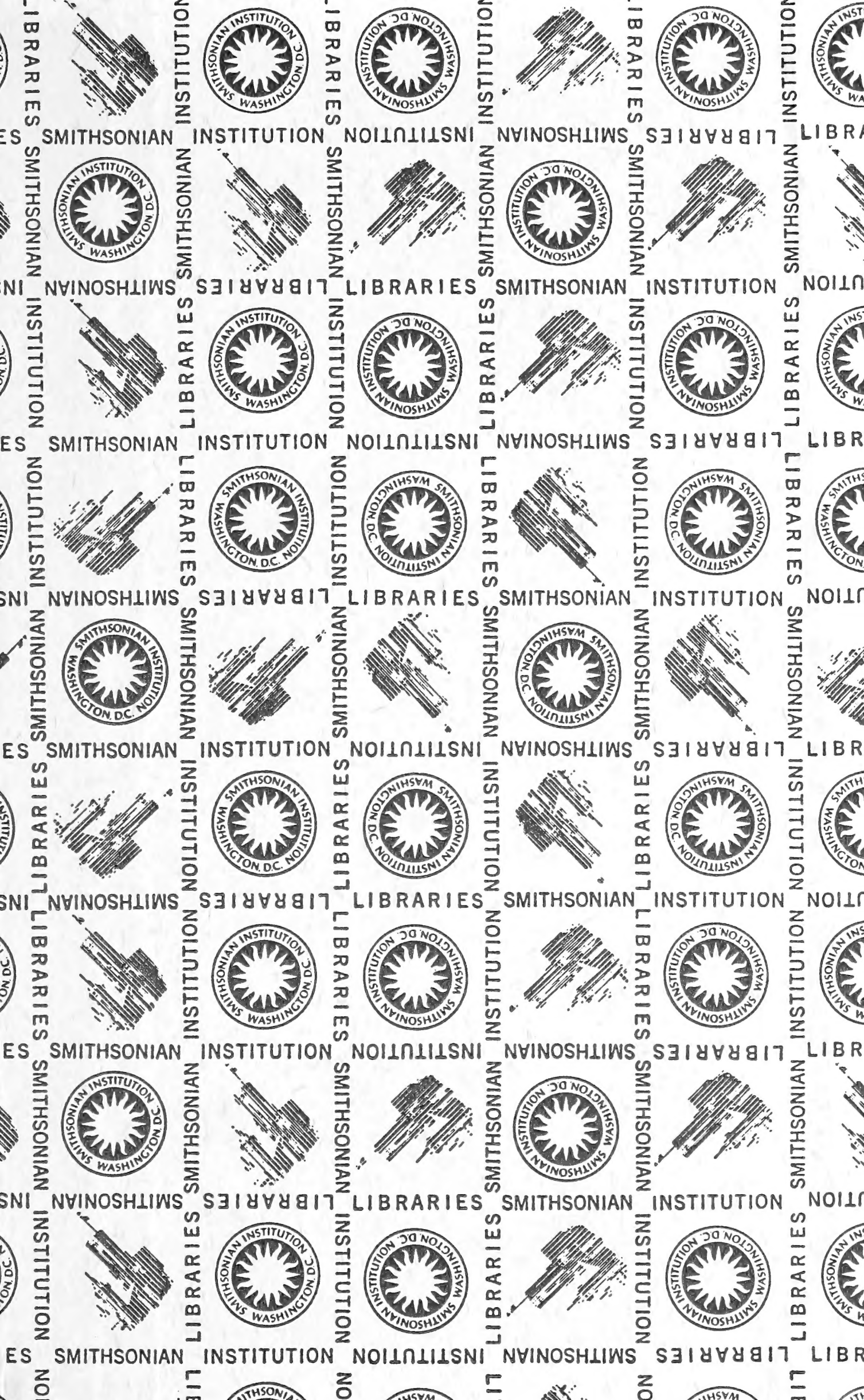
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